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Marine Flora and Fauna of the Eastern United States

Copepoda, Cyclopoida: Archinotodelphyidae, Notodelphyidae, and Ascidicolidae

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U.S. Department of Commerce

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The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R.I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts. Geographic coverage of the "Marine Flora and Fauna of the Eastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Florida, but can vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums.

The "Marine Flora and Fauna of the Eastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

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Marine Flora and Fauna of the Eastern United States

Copepoda, Cyclopoida: Archinotodelphyidae, Notodelphyidae, and Ascidicolidae—Associates of Ascidians

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ABSTRACT

This manual includes an introduction to the general biology, a selected bibliography, and an illustrated key to 11 genera and 17 species of copepods of the Crustacea, Subclass Copepoda, Order Cyclopoida, Families Archinotodelphyidae, Notodelphyidae and Ascidicolidae, associated with ascidians from the Atlantic Coast of the United States. Species distributed from the Gulf of Maine to Long Island Sound are emphasized. An annotated systematic list, with statements of the world distribution and new records of association with hosts, and a systematic index are also provided.

Introduction

The 8000 to 10,000 species of Crustacea belonging to the Subclass Copepoda occupy many niches in the ecosphere (Bowman and Abele 1982). Copepods are small, often less than 0.5 mm and rarely exceeding 10 mm in length (Kaestner 1970). They lack compound eyes and a carapace, although a cephalic head shield drawn out as an anteromedial rostrum is characteristic. Their segmented bodies are usually divided into a broad forebody and a narrow hindbody, separated by a major body articulation. In some, however, the taper of the body is more gradual. The genital apertures are on the last thoracic segment. There are 5 pairs of cephalic appendages and up to 7 pairs of thoracic appendages, the structure and numbers serving as important diagnostic features in classification. The postgenital abdominal segments of the hindbody never bear appendages, but two caudal rami extend from the posteriormost segment which includes the telson. The development of a copepod includes a series of naupliar and copepodid stages.

Most of the copepods are benthic, demersal, or planktonic free-living organisms in freshwater, estuarine or marine habitats. Some are free-living in such semiterrestrial habitats as wet moss, moist soils or leaf litter (Reid 1986). Many species have developed the capability of living as ectosymbionts or endosymbionts of other marine invertebrates or freshwater and marine fish (Gotto 1979; Kabata 1979). As might be expected, the bodies and appendages of copepods have undergone extensive adaptive morphological changes in concert with their radiation into so many different habitats. Symbiotic species, for example, with their needs to emphasize modes of attachment to a host and enhanced reproduction, may lack many of the defining characters of the Copepoda given above and their affinities with the group may only be determined by studying their developmental stages (Kaestner 1970). Gotto (1979), Kabata (1979) and Marcotte (1982, 1986) discuss the evolution of the diversity of body forms in the Copepoda and speculate on the different modes of feeding, locomotion, reproduction, and development required for their diverse life styles.

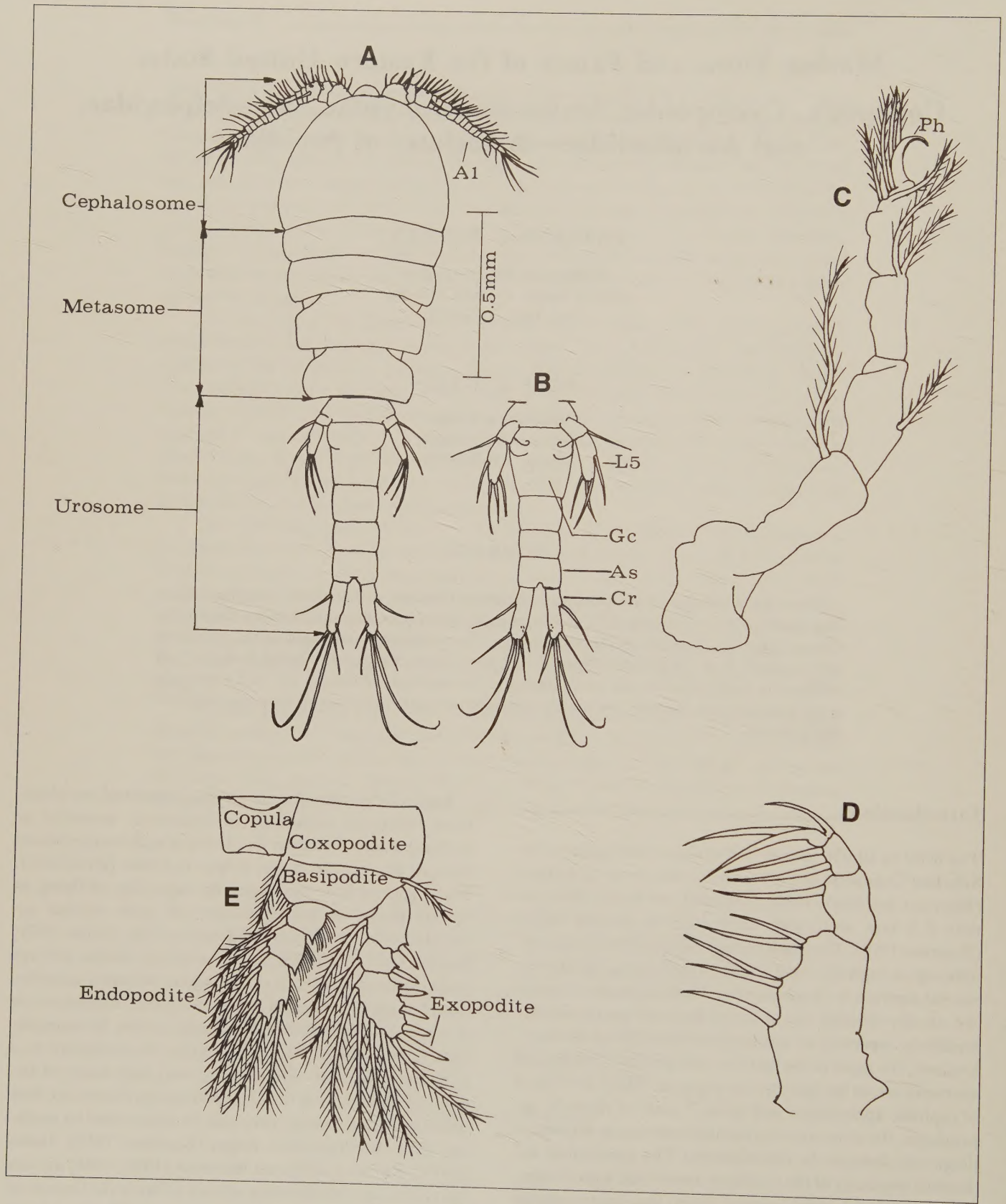


Figure 1

Pararchinotodelphys gurneyi, female; (**A**) habitus, dorsal view, showing divisions of body; (**B**) urosome, ventral view, showing segmental composition, caudal rami and fifth legs; (**C**) antenna with terminal prehensile hook; (**D**) maxilliped; (**E**) first leg with components labelled. As = anal segment; A1 = first antenna (antennule); Cr = caudal ramus; Gc = genital complex; L5 = fifth leg; Ph = prehensile hook.

The order Cyclopoida is one of the 8 orders of the subclass Copepoda (Kabata 1979; Marcotte 1982) and contains about 450 species (Bowman and Abele 1982). In this classification, still controversial, the other orders are the orders Calanoida, Harpacticoida, Misophrioida, Mormonilloida, Monstrilloida, Poecilostomatoida, and Siphonostomatoida. The copepods in the orders Cyclopoida and Poecilostomatoida differ from those in the other orders by universally possessing uniramous antennae (the second pair of appendages of the cephalon) rather than biramous antennae. While some copepods in the order Siphonostomatoida also have uniramous antennae, others have biramous antennae with extremely reduced exopodites. Cyclopoida and Poecilostomatoida differ from all Siphonostomatoida by having an open buccal cavity, rather than a siphonlike extension, containing buccal stylets and formed by fusions of the labrum and labium. The major differentiating characters between the orders Cyclopoida and Poecilostomatoida relate to the structure and function of the mandibles; the cyclopoids are basically gnathostomous (having biting or chewing mandibles) rather than poecilostomous (having falcate nonbiting mandibles or none) (Kabata 1979).

In the following brief diagnostic discussions, significant anatomical terms used in the keys are in boldface type and are explained in the text; an index to these is provided on p. 38.

The order Cyclopoida is an assemblage of free-living benthic, demersal or planktonic freshwater and marine species and many symbiotic species. Three of the families in the Cyclopoida, the families Archinotodelphyidae, Notodelphyidae, and Ascidicolidae, are marine symbionts in ascidians (there are a few records of occurrences in other invertebrate hosts) and are the subjects of this manual. The other three families which we include in the Cyclopoida are free-living species: the family Cyclopinidae, benthic or demersal in marine littoral zones; the family Cyclopidae, benthic, demersal or planktonic in freshwater or, less commonly, in the marine littoral zone; and the family Oithonidae, planktonic in the marine littoral and oceanic pelagic zones.

In general, an adult female cyclopoid copepod has its body segments organized as in most Crustacea into explicit functional regions, the **tagmata**. The term **segment** is used here to denote a major section of the body distinguished by clear articulations or by the presence of one pair of bilaterally arranged appendages. In the least modified cyclopoid females, as in females of the family Cyclopinidae or Archinotodelphyidae (Fig. 1A), the tagmata consist of a **cephalosome** bearing paired appendages consisting, from anterior to posterior, of the pre-oral cephalic antennules and antennae, the post-oral cephalic mandibles, maxillules and maxillae, and the thoracic maxillipeds, a **metasome** (Fig. 1A) of four free thoracic segments, each with a pair of biramous swimming legs, and a five-segmented **urosome** (Fig. 1, A and B). The urosome, set off from the metasome by the major body articulation, is composed of the segment of the reduced fifth legs (= the sixth thoracic segment), a genital complex (= the seventh thoracic segment fused with the first abdominal segment) which has a ventral gonopore and lateral or dorsolateral oviducal apertures, from which ovisacs are suspended at times of reproduction, and three additional abdominal segments. The least modified males of the order Cyclopoida are distinguished from females in their body segmentation only by having six segments in the urosome rather than five. Their genital segment (= the seventh thoracic segment), which bears small sixth legs not present in females, remains free of the first abdominal segment. In both sexes, the terminal abdominal element (= the **anal segment**) includes the telson with its pair of posterior caudal rami and dorsally directed anus. The **caudal rami** are flattened protrusions, each of which has four terminal, plumose setae as well as one small dorsal and one small lateral seta.

The forebody, consisting of the cephalosome and the metasome, is often referred to as the **prosome** (Gooding 1957) and is wider than the urosome. This arrangement in cyclopoids, whereby the major body articulation falls in front of the segment of the reduced fifth legs, is known as the podoplean condition. This contrasts with the gymnoplean condition of copepods of the order Calanoida in which the major body articulation falls posterior to the segment of the fifth leg and the urosome, therefore, bears no appendages (Giesbrecht 1892; Marcotte 1982).

As might be expected from the long evolutionary history of the Copepoda, none of the extant species of the order Cyclopoida can be considered archetypical with respect to its appendages. However, many investigators (Schellenberg 1922; Lang 1946, 1949; Lindberg 1952; Illg 1955, 1958; Dudley 1966) have recognized that species of the family Cyclopinidae have more appendicular features that might be referable to ancestral cyclopoids (plesiomorphic characters) than representatives of any other family in the order Cyclopoida. The most basic features of the cyclopoid appendages which are listed below, therefore, draw upon those characters which might be found in some species of cyclopinid. It is recognized, though, (Illg 1955; Dudley 1966) that extant species of the Cyclopinidae actually show mixtures of generalized and specialized characters.

In cyclopinids, the antennule is uniramous and has 10 to 26 segments. It is geniculate in males and has locking distal articulations used in holding the female during copulation. The uniramous antenna is 4-segmented, consisting of a 2-segmented protopodite and a 2-segmented endopodite, armed apically with setae only. The buccal cavity is open. There is a well-developed labrum anchored anterior to the mouth, but only a small labium, possibly represented in part by paired lobes called paragnaths posterior to the mouth. The biramous mandible has a 2-segmented protopodite and a biramous palp with a 2-segmented endopodite and an exopodite of up to 4

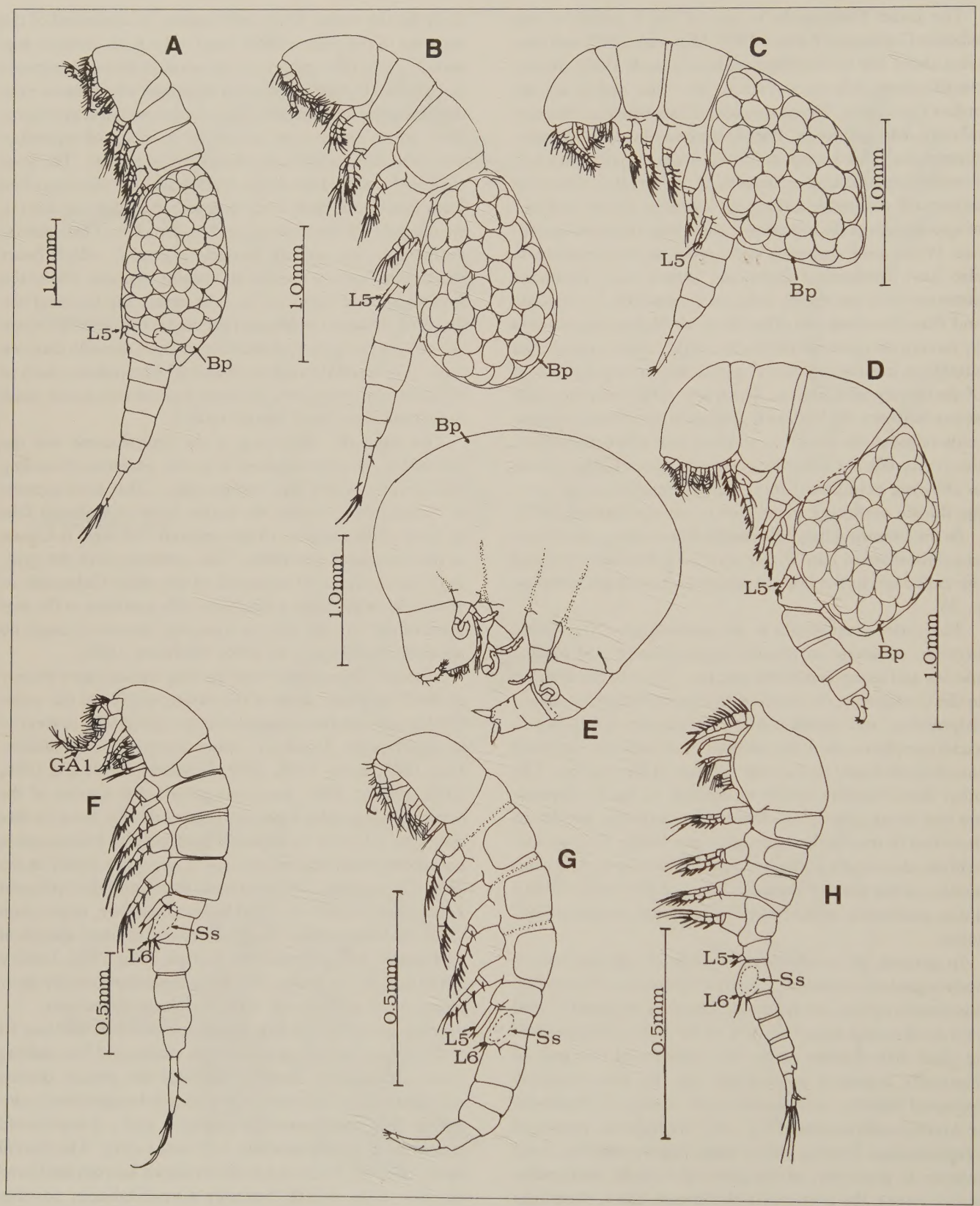


Figure 2

Lateral views of representative females and males of Notodelphyidae; (**A**) *Notodelphys monoseta*, female; (**B**) *Doropygopsis longicauda*, female; (**C**) *Doropygus laticornis*, female; (**D**) *Pachypygus macer*, female; (**E**) *Gunenotophorus curvipes*, female; (**F**) *Doropygopsis longicauda*, male; (**G**) *Doropygus laticornis*, anamorphic male; (**H**) *Doropygus laticornis*, metamorphic male. Bp = broodpouch; GA1 = geniculate antennule; L5, L6 = fifth and sixth legs; Ss = spermatophoral sac.

segments. The mandible is gnathostomous with a medial, coxopodal, gnathal plate which can work under the labrum. The biramous maxillule has a 2-segmented protopodite with medial setose endites as well as a lateral epipodite and a 1-segmented endopodite and exopodite. The uniramous maxilla is 6-segmented. The basal 3 segments have setose endites and there is a claw, as well as setae, on the endite of the third segment. The 3 small, distal segments, armed with setae, are considered by some investigators to be an endopodite, although there is no ontogenetic reason to consider that this appendage is biramous. The maxilliped of the first thoracic segment of the body is uniramous and has up to 7 segments and up to 18 setae apportioned to the segments. The four pairs of thoracic, biramous swimming legs are similar in the Cyclopinidae and the Archinotodelphyidae (Fig. 2E). These appendages have flattened **protopodites**, each with a clearly indicated **coxopodite** and **basipodite**, the latter supporting the two **rami**, the 3-segmented **exopodite** and **endopodite**. The endopodite is armed only with setae while the exopodite has lateral and apicolateral spines and medial and apicomedial setae. There is a quadrate plate, called the **copula** or **intercoxal plate**, which links the contralateral legs on each metasomal segment and allows the paired legs to serve as a single unit during swimming. The uniramous, 2- to 3-segmented fifth legs on the first urosomal segment have up to 7 setae. The sixth legs, found only in males, consist of apposed subtriangular plates on the ventral surface of the second urosomal segment. Each is armed with 3 setae.

Diagnoses and Relationships of Families of Cyclopoid Ascidicolous Copepods

Family Archinotodelphyidae

The family Archinotodelphyidae is the smallest family of ascidicolous copepods, consisting of only three genera and six species. These live in simple ascidians of several families (Hansen 1923; Lang 1949; Illg 1955; Monniot 1968, 1987), and, paradoxically, one species, *Nearchinotodelphys indicus* Ummerkutty (1960), in a boring bivalve mollusc. The family is of interest with respect to the phylogeny of Copepoda because of its suggested position evolutionarily between the many marine representatives of the cyclopoid family Cyclopinidae and the now substantially numerous species of the symbiotic family Notodelphyidae (Illg 1955; Dudley 1966).

A major common feature of the family Archinotodelphyidae and the family Cyclopinidae is the generalized cyclopoid **habitus** or general aspect of bodily organization of the females. In the northeastern United States, the female of *Pararchinotodelphys gurneyi* Illg (1955) from the ascidian *Styela partita* is a representative example in regard to its habitus (Fig. 1, A and B). The urosome may, however, be variable among archinotodelphyid genera. Lang (1949) reported the urosome of female *Archinotodelphys typicus* as having 6 segments. There is no broodpouch and the embryos are carried in external ovisacs.

The appendages of archinotodelphyids differ from those of cyclopinids in the following ways: the antennule has 15 to 17 segments rather than 10 to 26 as in cyclopininds; the antenna (Fig. 1C), although 4-segmented as in cyclopinids, has fewer setae and an apical, articulated, prehensile hook, which is absent in cyclopinids. The prehensile hook is the only clear appendicular modification of archinotodelphyids related to their symbiotic existence in ascidians. The maxillule, peculiarly, may be more specialized in cyclopinids than in archinotodelphyids by having fewer endites on the protopodite and, in some cases, by lacking the epipodite possessed by all archinotodelphyids. The maxilliped (Fig. 1D) has 3 to 5 segments and fewer setae than do cyclopinids. In no cyclopinid does the maxilliped have less than 5 segments and, in some species, may have as many as 7 segments.

Similarities in appendages between archinotodelphyids and cyclopinids exist in the structure of the mandible, maxilla, and the metasomal legs (Fig. 1E), which conform in all details of segmentation and have a similar armature. In addition, the males, known only in *Archinotodelphys profundus* Monniot and *Nearchinotodelphys indicus* Ummerkutty, have geniculate antennules as do cyclopinid males.

Family Notodelphyidae

The Copepoda of the family Notodelphyidae have been almost universally described as inhabitants of ascidians although some descriptions of species have given as their provenance washings or mud from unspecified marine collections or collections from other colonial marine invertebrates that could be confused with compound ascidians.

One major criterion defines all females of the species of the family Notodelphyidae: the formation of an internal broodpouch (Fig. 2, A through E) within which the embryos develop until they are released for the free-living phases of the life cycle. Another feature defines both males and females of the family: the presence of a prehensile hook on the apex of each uniramous antenna (Fig. 3, B and C). Both of these are doubtlessly basic adaptations to help adults or their developmental stages avoid the filter-feeding entrapment mechanisms and the powerful flushing and back-flushing which occur in the ascidian's branchial basket. These defining characteristics of the Notodelphyidae, however, persist even in those highly modified species which occupy loci in the ascidian host where they or their embryos are not subject to filter-feeding entrapment.

The vividly colored eggs or embryos in the broodpouches of females are easily seen when the ascidian hosts are dissected and, largely because of this, adult females are much better known than are the smaller, white or yellowish

males. Features of identification of notodelphyid genera are usually based on females and the characters used in the key in this manual are so restricted. The habitus is one of the most important features for the identification of the genus of a notodelphyid female. The presence of the broodpouch causes the bodies (Fig. 2, A through E) to deviate to varying degrees from the habitus of the generalized cyclopoid female. The least modified females of Notodelphyidae, living in the branchial baskets of solitary ascidians, are those of species of *Notodelphys* (Fig. 2A), which are very active and can leave the ascidian under adverse conditions. The broodpouch does show some bulging laterally and dorsally and occupies both the fifth and sixth thoracic segments (= segments of the fourth and fifth legs). Because the segment of the fifth leg is incorporated in the pouch and the major body articulation falls behind it, the urosome carries no legs and a secondary gymnoplean condition exists, a peculiarity in the Cyclopoida.

As other examples, species of *Doropygopsis* (Fig. 2B), *Doropygus* (Fig. 2C), and *Pachypygus* (Fig. 2D) are laterally compressed and have large gibbous broodpouches that occupy only the last metasomal segment (= segment of the fourth legs). Because the fifth legs are found on the first urosomal segment, species of these genera show the podoplean condition. The development of this large pouch causes the prosome in these females to tilt ventrally relative to the urosome and, in all of these genera, a progression of restrictions in motility accompanies its formation. No adult females of species in these genera are known to leave their hosts. In species in other genera, also found in branchial chambers of solitary ascidians, the broodpouch may extend more anteriorly into the metasomal segments or the body may be grossly inflated and a lobed broodpouch may superficially cover much of the fused metasome as in *Gunenotophorus* (Fig. 2E). Fifth legs are absent in species of this genus.

Adult females of species which occupy cysts have the most profound modifications of body form among notodelphyid associates of solitary ascidians. In females of such species as *Scolecodes huntsmani*, living in cysts in the subendostylar blood vessels of its hosts (Illg 1958; Dudley 1968) and *Scolecimorpha joubini*, living in cysts in the tunic wall (Illg and Dudley 1961), the bodies are vermiform and show much fusion of segments. Broodpouches are very capacious and long, occupying only an extended sixth thoracic segment in *S. huntsmani* and the whole lengthened metasome in *S. joubini*. But however much the bodies of notodelphyids in cysts in solitary ascidians are modified, it is in the notodelphyid associates of compound ascidians where specialization reaches extremes. All of these species from compound ascidians have bodies that are so changed toward a vermiform or globular habitus that it is sometimes difficult even to recognize that they are copepods. Among these, the species that occupy the branchial baskets of zooids are less modified than those that are found in the common cloaca, postabdomens of zooids, or the matrix of the colony (Illg and Dudley 1961, 1965). Representatives of these extremely modified notodelphyids from cysts in solitary ascidians or from compound ascidians have not as yet been collected from the Atlantic coast of North America.

Although we have insufficient material to use males of the Notodelphyidae in the key, we have collected a male of *Doropygopsis longicauda* (Fig. 2F) and males of two species of *Doropygus*, *D. laticornis* (Fig. 2, G and H) and *D. curvatus*. A few generalities are given here in the expectation that other males in the family will be found. Additional information on males in this family can be found in Dudley (1966, 1986) and in the discussion of Male Dimorphism below. A caveat must be given that the mere physical presence of both males and females in a single specimen of a host is not a sufficient criterion for a common specific identity because concurrent infestation of a single ascidian by more than one species of notodelphyid can occur.

The males of species of such genera as *Doropygopsis* and *Notodelphys* are found in the branchial baskets of their hosts but have been seen by us to leave their hosts and can swim actively. They have a generalized cyclopoid habitus, very similar to that of males of cyclopinids or archinotodelphyids. They are about 1/2 to 2/3 the lengths of their corresponding females but differ from them by having 6 urosomal segments and by having **sixth legs** (Fig. 2F) on the ventral surface of the second urosomal segment. Two spermatophoral sacs (seminal vesicles) are visible within the second urosomal segment and the sixth legs overlie the two spermiducal openings from these sacs. Otherwise, except for their **geniculate** grasping antennules (Fig. 2F), these males conform closely in their appendicular structure to the females, and can, in fact, be identified by using the characters of the appendages of the females.

In species of *Doropygus*, there are anamorphic, creeping males, which, like the female, have lost considerable motility and which are only about 1/2 the length of the females (Fig. 2G). Their appendages are very similar to those of the females, but, unlike the males of *Notodelphys*, anamorphic males of *Doropygus* do not have geniculate antennules. Such males are found in the branchial baskets of their hosts or, even more commonly, on the peribranchial wall in the atrium along with various immature copepodid stages. Neither they, nor the late copepodid stages, leave the host. However, in addition to the anamorphic male, a second kind of male has been found in *D. laticornis*, appearing by metamorphosis from fifth copepodid males placed in cultures. These males (Fig. 2H) have a cyclopoid habitus and legs adapted for swimming, and can indeed swim actively, but their mouthparts are so reduced that it is unlikely that they can feed. The development of male dimorphism in this and other species of Notodelphyidae is discussed below.

In addition to using the habitus and the segmental modifications of the body as described above, the features of the cephalosomic appendages (Fig. 3, A through G) are primarily invoked in identifying the females of notodelphyids to genus and species. The identification may also depend on the structure of the first through fifth legs (Fig. 4, A through E) and the caudal rami (Fig. 4, D, F, and G).

In making these determinations, the posture, contours, segmentation of the appendages and their features of armature and ornamentation furnish useful characters. **Segmentation** concerns the numbers of constituent articulated elements of appendages, which we refer to as **segments**, but which could also be called articles or podomeres. **Armature** consists of **spines** (shorter, stouter elements with elaboration, if any, consisting of a row or rows of spinules or tooth-like projections [Fig. 4A] and **setae** [Figs. 3A, 4A], longer and more flexible and slender, with elaborations, if any, consisting of fine hair-like processes in marginal rows). Such a fully elaborated seta is referred to as **plumose** (Fig. 4A); **aesthetascs**, localized on the antennules, and thought to be chemoreceptors, are flattened, blunt-ended, transparent elements (Fig. 3A); and **hooks** or **claws**, more massive, are suggestive of prehensile function in most cases (Fig. 3, B and C). Characteristic placements of spines and setae on the various appendages serve as diagnostic characters. **Ornamentation** consists of specializations of any cuticular surface, such as hairs (Fig. 4A), spinules (Fig. 4E), flanges, pits, and pores.

There is an extremely wide range of structural variation in appendages through the family Notodelphyidae. Appendicular characteristics that differ little from those of the generalized cyclopoid, as well as highly specialized features, can be found in the same species. However, notodelphyids that have very intimate relationships with their host ascidians, such as those living in cysts in solitary ascidians and all of those occupying compound ascidians, have such specialized appendages that most similarities to the generalized cyclopoid have been lost. In adult females of many of these, one or more pairs of appendages may even be missing and it is often difficult to determine homologies of the persistent appendages or their components. Only developmental evidence and the retention of the defining familial characteristics of prehensile antenna and broodpouch allow the placement of these species in the family Notodelphyidae.

In the least modified Notodelphyidae, found in the branchial baskets of solitary ascidians, the appendages have a number of points of similarity to the appendages of the species of the family Archinotodelphyidae but are somewhat further removed from those of the family Cyclopinidae by reductions in segmentation and setation. Evolutionarily, the Archinotodelphyidae appears to lie between the other two families. This relationship between the three families has been discussed in detail by Illg (1955, 1958) and Dudley (1966).

In comparing the appendages of the notodelphyids with those of the archinotodelphyids, we use only the features of species of the least modified genera *Notodelphys*, *Doropygopsis*, *Notodelphyopsis*, and *Doropygus*. As an aid to understanding the structure of appendages and caudal rami we present illustrations for *Doropygus demissus* (Figs. 3, A through G; 4, A through G) as representative of the genus *Doropygus* whose species are the most commonly encountered notodelphyids in the eastern United States.

Similarities in the appendages in the most generalized notodelphyids and archinotodelphyids lie in the presence of the articulated, prehensile hook on the apical segment of a uniramous antenna (Fig. 3, B and C); concurrence in the overall construction of the biramous mandible (Fig. 3D) and the biramous maxillule (Fig. 3E), although there are differences in the two families in numbers of setae on protopodites and rami; the 4 pairs of metasomal legs conform to the general cyclopoid type of segmentation and armature. In *Doropygus* (Fig. 4, A through C), however, the proportions of the rami of the legs differ from those of cyclopinids and archinotodelphyids. In legs 2–4 there can be consolidations of the apical and middle segments of the endopodites, and the elements of armature on the lateral margins of exopodites are more like setae than spines. The caudal rami of *Notodelphys*, *Doropygopsis*, and *Notodelphyopsis* have long terminal setae and shorter separate dorsal and lateral setae, as in archinotodelphyids, but, in *Doropygus* (Fig. 4, D, F, and G), the terminal setae are greatly reduced and the rami are somewhat curved and tapered.

There are a number of differences in appendages of the most generalized notodelphyids and those of archinotodelphyids. These are as follows: There is a trend in notodelphyids to reduction in the segmentation of the uniramous antennule (Fig. 3A), the least-modified notodelphyid females have 9 to 15 segments compared with 15 to 17 segments in archinotodelphyids; the antennule in male notodelphyids is not geniculate except in species of *Notodelphys*, *Doropygopsis*, and *Notodelphyopsis*; the antenna (Fig. 3, B and C) has fewer setae and the number of segments is reduced from 4 to 3, although *Doropygopsis* does have an indication of a partially fused fourth apical segment; and a maxilla (Fig. 3F) which is 5-segmented rather than 6-segmented as in archinotodelphyids because of a fusion of the 2 basal segments, indicated by a nonfunctional articulation in *Doropygopsis*. There are still 3 small apical segments in the maxilla as in archinotodelphyids, a portion of the appendage that is occasionally referred to as an "endopodite." In some species of notodelphyids, as in those of some species in the genus *Doropygus*, the characteristic claw on the second segment becomes seta-like; the maxilliped (Fig. 3G) in notodelphyids never has more than 3 segments and can even be 2- or 1-segmented, thus overlapping the range of 3–5 segments in archinotodelphyids. There are fewer setae on the terminal segment of

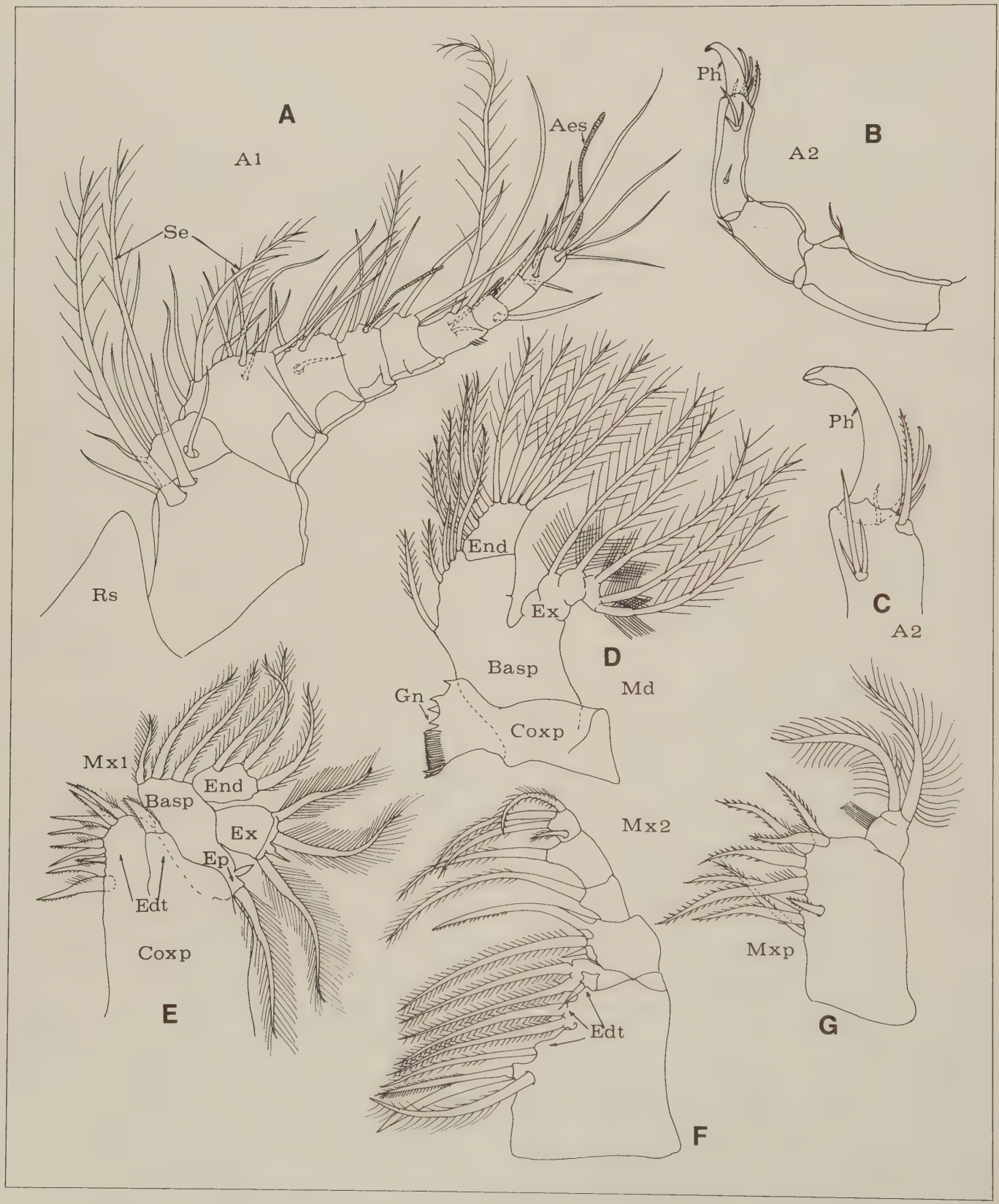


Figure 3

Appendages of cephalosome, *Doropygus demissus*, female; (**A**) antennule; (**B**) antenna; (**C**) apex of distal segment of antenna; (**D**) mandible; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped. Aes = aesthetasc; A1 = first antenna (antennule); A2 = second antenna (antenna); Basp = basipodite; Coxp = coxopodite; Edt = endite; End = endopodite; Ep = epipodite; Ex = exopodite; Gn = gnathobase, Mx1 = first maxilla (maxillule); Mx2 = second maxilla (maxilla); Mxp = maxilliped; Ph = prehensile hook; Rs = rostrum; Se = seta.

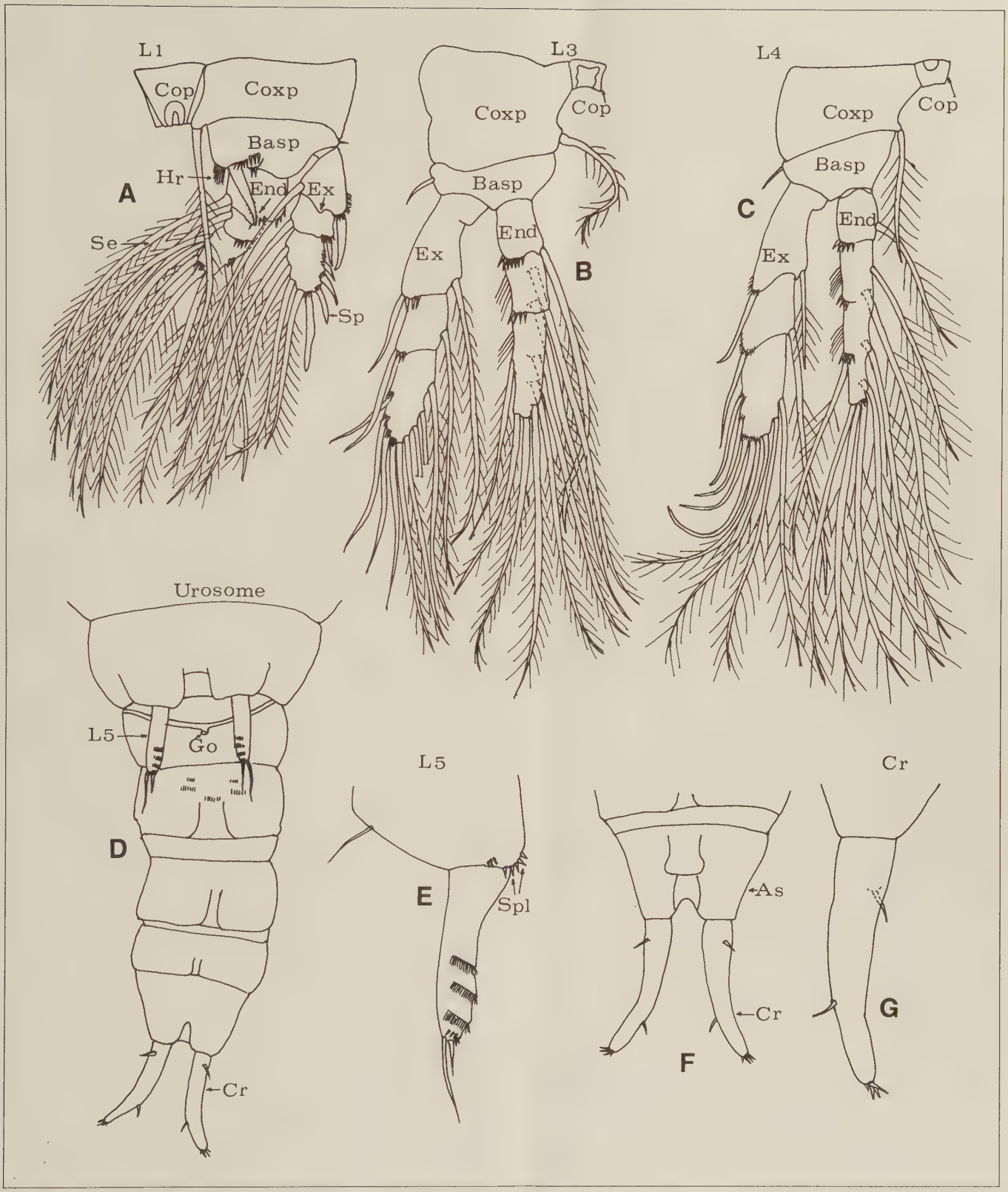


Figure 4

Appendages of metasome and appendages of urosome, *Doropygus demissus*, female; (**A** through **C**) first, third, and fourth legs; (**D**) urosome, ventral view; (**E**) fifth leg; (**F**) anal segment of urosome with caudal rami; (**G**) caudal ramus. As = anal segment; Basp = basipodite; Cop = copula; Coxp = coxopodite; Cr = caudal ramus; End = endopodite; Ex = exopodite; Go = genital opening; Hr = hair; L1, L3, L4, L5 = first, third, fourth, and fifth leg; Se = seta; Sp = spine; Spl = spinule.

the maxilliped in notodelphyids; the fifth legs (Fig. 4, D and E), when present in notodelphyids, are uniramous and 2-segmented as in archinotodelphyids but never bear more than 1 lateral seta on the basal segment and 2 setae on the distal segment, compared with 1 seta on the basal segment and 4 on the distal segment in archinotodelphyids.

Family Ascidicolidae

The family Ascidicolidae includes six subfamilies of ascidicolous copepods: Ascidicolinae, Botryllophilinae, Buprorinae, Enterocolinae, Enteropsinae, and Haplostominae (Illg and Dudley 1980). A seventh subfamily, Enterognathinae, includes copepods that are associated with echinoderms and hemichordates but which show many similarities to the subfamilies associated with ascidians. The family Ascidicolidae, unlike the family Notodelphyidae, has no all-encompassing features which define it unequivocally. However, the familial concept (Illg and Dudley 1980) derives from the recognition of interlocking evolutionary trends, most particularly as they relate to the many degrees of adaptation of the females to a symbiotic existence.

Drawing upon the information in Illg and Dudley (1980), Ooishi (1980) and Ooishi and Illg (1977), we can present comparisons of the structure of the ascidicolid subfamilies. No female ascidicolid has a generalized cyclopoid habitus. Only females in the subfamily Buprorinae (Fig. 5A) have broodpouches like those in the Notodelphyidae; all of the other female ascidicolids carry external ovisacs. The bodies of female ascidicolids range from those with well-articulated body segments and heavily setiferous or spiniferous appendages, somewhat referable to the cyclopoid type except for the extensive development of the fifth legs (subfamily Ascidicolinae), to those whose metasomes show some degree of segmental fusion and inflation and whose appendages show more reductions in segmentation and armature (subfamily Botryllophilinae; Fig. 5, B through D) to those with extensive fusions of body segments, an overall grub-like appearance with a trend toward elongation and enlargment of the body, some losses of cephalosomic appendages and specialization of the appendages which remain (subfamilies Enterocolinae, Enterognathinae, Enteropsinae, and Haplostominae; Fig. 5, E and F).

The fact that different clusters of these subfamilies share particular characteristics of the appendages in an interwoven pattern justifies the concept of an overall cohesiveness of the family Ascidicolidae. Thus, females in the subfamilies Ascidicolinae, Buprorinae, and Botryllophilinae have antennules of 3–7 segments which are provided with many setae of moderate length, but, in the other subfamilies, the antennule is an unsegmented to weakly 2-segmented tapered lobe with a reduced number of small setae. The antennule is missing in species of *Lequerrea* in the Enterocolinae. The antenna is uniramous and 2- to 3-segmented in all of the subfamilies, but the armature is generically distinct. Only the females of Ascidicolinae have an apical articulated prehensile hook on the antenna which resembles that of the Notodelphyidae. Females of *Haplostomides* and *Haplostoma* species in the Haplostominae do have apical antennal spines that are moderately hooked, but they appear to be different from hooks in notodelphyids. The mandible in the subfamilies Ascidicolinae, Botryllophilinae, Buprorinae, and Enterognathinae shows the basic gnathostomous derivation of the family by possessing a medial coxopodal gnathal plate. In the first two subfamilies, the mandible has a uniramous 1- to 2-segmented setiferous palp but the palp is reduced to a single setiform process in the latter two subfamilies. The mandible is absent in the Enterocolinae and Enteropsinae and is represented by a very small unsegmented to 4-segmented lobe, usually with a few setae, in the Haplostominae. The maxillule is lacking in females of species of *Haplostoma*, *Haplostomella*, and *Haplosaccus* in the Haplostominae, but in *Haplostomides* in this subfamily and in all other subfamilies the maxillule consists of a basal piece that bears setae medially and an unsegmented palp with apical setae. The numbers of setae vary according to genus. The basal component of the maxillule resembles the coxopodite and endite of the basic notodelphyid maxillule but the palp is specialized. The maxilla, lost or reduced to a very small setiferous lobe in the Haplostominae, shows many similarities between *Ascidicola* in the Ascidicolinae and all species in the Buprorinae, Enterocolinae, and Enterognathinae. In these, there is a large basal segment with a medial setiferous or spinelike endite and 1 or 2 distal segments, with the apical segment drawn out as a hook. The maxilla of Enteropsinae is 2-segmented and the endite on the basal segment is lacking, but otherwise it has many similarities to the maxilla in the other subfamilies listed above. This prehensile maxilla differs considerably from the maxillae of female *Styelicola* in the Ascidicolinae and all species in the Botryllophilinae, in which the basal segment has several endites bearing long setae and where there are up to 3 distal segments, also armed with setae. This more closely resembles the appendage of the Notodelphyidae. The maxilliped is not present in Enterocolinae, Enteropsinae, and Enterognathinae but is found in the other subfamilies and can have one of two very different forms: 1) in Buprorinae and Ascidicolinae it is an unsegmented lobe with medial and apical setae, reminiscent of the maxilliped in some of the more modified Notodelphyidae; 2) in the Haplostominae and Botryllophilinae it is a massive prehensile appendage of 3 segments with a prehensile hook-like process on its distal segment and is unlike any maxilliped in the Notodelphyidae.

The 4 pairs of legs of the second through fifth thoracic segments show patterns of segmentation and armature which are generically distinct. None of these legs is

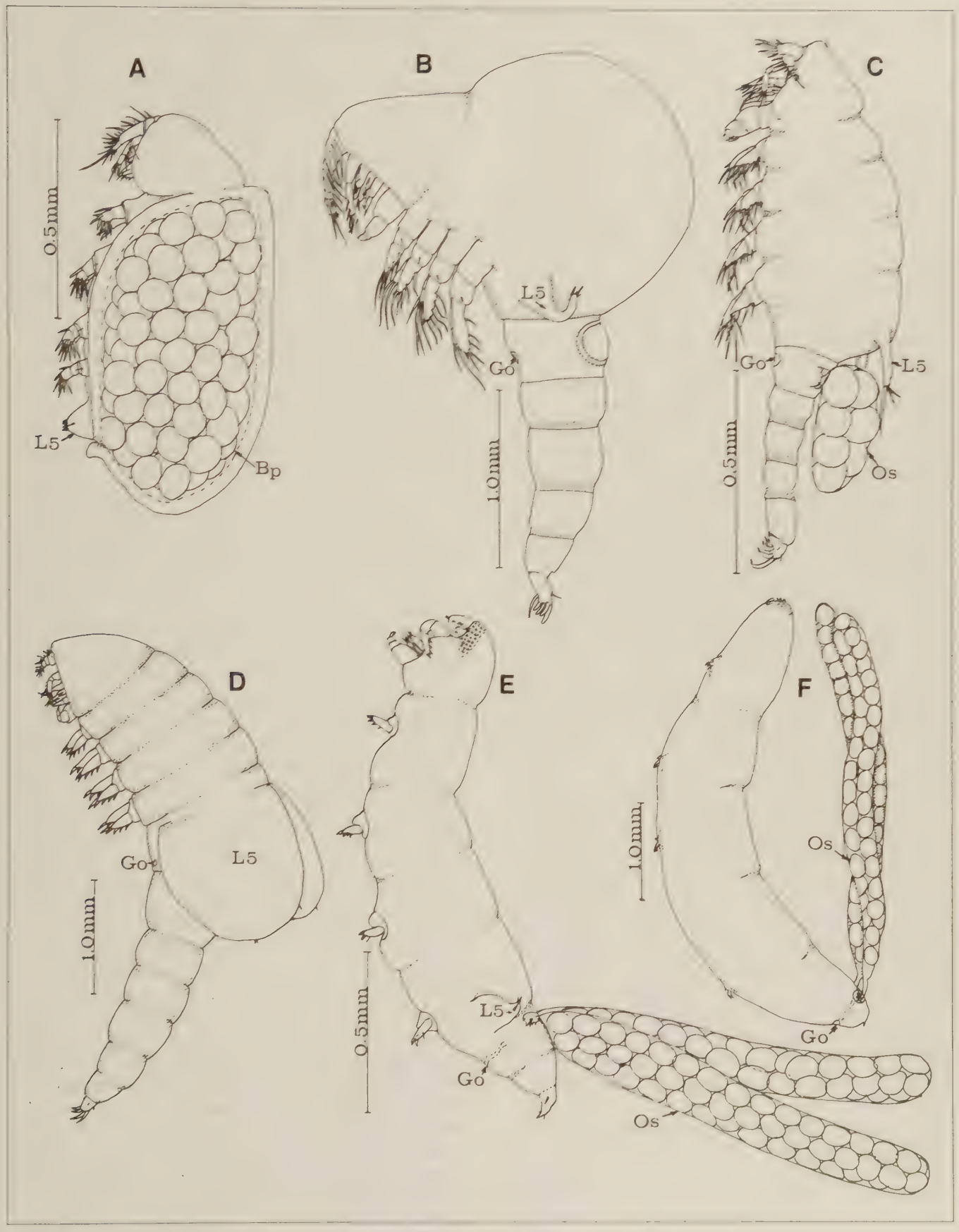


Figure 5

Lateral views of representative females of Ascidicolidae: (**A**) *Buprorus loveni*; (**B**) *Botryllophilus norvegicus*; (**C**) *Botryllophilus* sp. from *Aplidium glabrum*; (**D**) *Schizoproctus inflatus*; (**E**) *Haplostomides amarouci*; (**F**) *Haplosaccus elongatus*.

missing in an ascidicolid female, unlike the situation in the most modified notodelphyids which usually lack one or more pairs of legs. The first through fourth legs are closest in their structure to the basic cyclopoid pattern in females of *Ascidicola* in having a 2-segmented protopodite and in being biramous, but their exopodites are only 2-segmented and bear spines only and the 3-segmented endopodites have both spines and extraordinarily long setae on their distal segments, thus differing from the pattern in free-swimming cyclopoids. Within the family Ascidicolidae, there is a range of specialization from the ascidicolin type to the very modified uniramous, spiniferous legs of some Haplostominae to those of the Enteropsinae with bulky, uniramous, 2-segmented legs which are armed distally with a retractile hook.

Except in the subfamily Enteropsinae, where the fifth legs are absent in females, and in *Haplosaccus* females (Haplostominae) where fifth legs are represented by a single seta, there is a trend within the Ascidicolidae to a displacement of the fifth legs to a more dorsolateral position than in the Notodelphyidae and a tendency for these appendages to become expanded by incorporating part of the body wall (Fig. 5, B through E). In most ascidicolid females, the fifth legs participate in stabilizing the bases of the external ovisacs or, if lamellate, overlie and shelter entire, shortened, flattened globose ovisacs. There is a considerable variety of caudal rami within the family. Caudal rami can be similar to those of cyclopinids or archinotodelphyids (Ascidicolinae), or they can be clawed (Botryllophilinae), or tiny pointed processes (Enteropsinae), or barely indicated lobes with very small setules or spinules or lacking armature (Enterocolinae, Enterognathinae, Haplostominae), or they are not set off from the end of the urosome at all (Buprorinae).

With the exception of the subfamily Buprorinae, males of at least one species in each of the subfamilies have been described (Canu 1892; Giesbrecht 1892; Monniot 1965; Illg and Dudley 1980; Ooishi 1980; Gotto et al. 1984; Ooishi and Illg 1977, 1986). The males in two species of *Haplostoma* are described as being of the creeping type (Ooishi and Illg 1977), but all of the other males of species of Haplostominae are swimmers. Virtually all of the males in the other subfamilies are also thought to be capable of swimming, but some have been described only from preserved specimens and have not been studied in life. If true, the ability of most ascidicolid males to swim actively could explain their rarity in the ascidians. We have not been able to find any males in our study of the Ascidicolidae on the Atlantic coast.

Except for a presumed male of *Schizoproctus*, illustrated by Sars (1921), which shows characteristics of segmental fusion and inflation in its body similar to the modified females, all of the other males described to date have a cyclopoid habitus with podoplean tagmosis, reduced fifth and sixth legs on the venter of the first and second urosomal segments, respectively, and setiferous caudal rami. Conservative features of the appendages in the swimming and creeping males include the 4–9 well-articulated segments in the antennules and the segmentation in legs 1–4 which approaches the cyclopoid pattern. However, the antennules are nongeniculate and are therefore more reminiscent of males of modified notodelphyid species than those of males of the Archinotodelphyidae or Cyclopinidae and there are some modifications of the legs, particularly the first legs, which are generically characteristic and specialized. The other appendages of male ascidicolids show subfamilial or generic characters. If an appendage is absent in the female of a given species, it almost always will be lacking in the male, too. One exception is seen in males of some species of *Haplostoma* which possess a small lobed setiferous maxilla, even though it is lacking in corresponding females (Ooishi and Illg 1977).

The males of *Ascidicola rosea* are reported as having head appendages very similar to those of the females (Monniot 1965), but sexual dimorphism is characteristic in the males from other subfamilies. The dimorphic features in males, compared with those in females, include: the larger numbers of segments in the antennule, its more profuse setal complement and, in the Haplostominae and Botryllophilinae, the many aesthetes; the lengthening and narrowing of the segments of the antenna and the presence of a distal antennary prehensile hook in males, but not females, of species of *Enterocola*; the loss or great reduction of the coxopodal gnathal plate of the mandible in males of species of *Botryllophilus*; the attenuation of the residual mandibular palp in *Botryllophilus* and species of *Haplostoma* and *Haplostomides*; the loss of the basal endite of the maxillule in the Botryllophilinae, Enteropsinae, Enterocolinae, and *Haplostomides* in the Haplostominae and the lengthening of the remnant of the palp or its setae; the great reduction of the maxilla in the males of Enterocolinae, Enteropsinae, and Botryllophilinae to simple lobes with one to several setae, very different from the appendage in the females; and the proportionate lengthening of the maxilliped and the enlargement of its apical hook in the Botryllophilinae and Haplostominae; the reduction of the fifth legs to, at most, a minute protrusion whose basal segment bears 1 lateral seta and a distal segment with 1 or 2 apical setae. In the male of *Mychophilus roseus*, the male has fifth legs even though fifth legs are absent in females (Gotto et al. 1984).

A critical comparison of males in different subfamilies of ascidicolids can lead to new ideas of their relationship. Such a study by Ooishi and Illg (1986) has suggested a much closer relationship between the subfamilies Botryllophilinae and Haplostominae, based on similarities in the armature and segmentation of the antennules, mandibular remnants, and maxillipeds in males, than could be determined by studying the modified adult females alone. Critical analyses of structure in the males also reinforce our ideas about the close relationship of the Notodelphyidae

and the Ascidicolidae. For example, the prehensile hook on the antennae of the males of species of *Enterocola* is very similar to that of Notodelphyidae, as are the fifth legs and other conservative features of segmentation and armature of the swimming legs.

The ascidicolids have become more specialized than notodelphyids in their adaptation of appendages for prehensile attachment. Little is known of their biology because they often live in such small or opaque ascidians that studying them in place is most difficult. We assume that they use the prehensile appendages to attach to their hosts or, in the case of males, to hold the females during copulation. Although most ascidicolids (except *Styelicola* females and *Enterocola* males) do not have a prehensile articulated hook on their antennae, they have other appendages which may serve the same function. In males and females of the Haplostominae and males of Botryllophilinae, the maxilliped is the most massive prehensile organ but, in females of Enterocolinae and Enteropsinae in which the maxillipeds are absent, the maxilla is a large, similarly developed attachment organ. On generic levels, legs may show various prehensile modifications and, in the Botryllophilinae, the caudal rami are clawed. There is no clear modification of the appendages of the subfamily Buprorinae for prehension, but only the females are known.

Biology

Associations With Ascidian Hosts

In addition to understanding the systematics and biology of the ascidicolous cyclopoid copepods, the researcher on these animals faces an additional challenge in needing to be cognizant of the systematics and biology of the hosts as well. The extent of host specificity varies among notodelphyids and ascidicolids and, as Gotto (1979) remarked, "few hard and fast rules can be applied." Although most species of ascidicolous cyclopoids occupy a single species of ascidian host (phylum Chordata, subphylum Urochordata [= Tunicata], class Ascidiacea), there are records of a single copepod species associating with two or more related species of ascidian hosts in the same genus, or associating with ascidian species in two or more genera of the same family, or occupying two or more unrelated species of ascidian hosts in different families or even orders (Illg and Dudley 1961, 1965; Ooishi and Illg 1977). Some of the rosters of unrelated hosts include older records and may stem from misidentifications of the hosts or the copepod associates (*see* Annotated Systematic List in this manual). Others, however, are real and may either result from the copepods' ability to sense required anatomical or physiological features even in ascidians that are not taxonomically close or they may just be cases of expediency if preferred hosts are not as accessible as substitute hosts at the times of infection.

There is no proven record of any ascidicolous cyclopoid species occupying both solitary and compound ascidians. However, in some genera, there are examples of species that associate with solitary ascidians even though their congeners associate only with compound ascidians. Examples from Ooishi and Illg (1977) are *Haplostoma gibberum*, *Haplostoma eruca*, *Haplostomella australensis*, and *Haplostomella halocynthiae* and from Illg and Dudley (1980; this report): *Enterocola laticeps*, *Botryllophilus norvegicus*, and a *Botryllophilus* species, all from solitary ascidians. Other species in these genera live in compound ascidians.

Within solitary ascidians, the most common locus for copepods is the branchial basket (= pharynx). This site is characteristic for Archinotodelphyidae and most females and males of Notodelphyidae, although creeping males in *Doropygus* are often found on the outside of the branchial wall and can move back and forth through the stigmata from the atrium to the branchial basket. Two species of notodelphyids occupy cysts in blood vessels of solitary ascidians, *Scolecodes huntsmani*, in the subendostylar blood vessel, and *Scolecimorpha joubini*, in blood vessels of the tunic. Some representatives of the Ascidicolidae can also be found in the branchial basket of their solitary hosts, but other sites where representatives of this family are found are the esophagus, stomach, intestine, or atrium. Females of the ascidicolids *Ascidicola rosea* and *Enteropsis chattoni* spend most of their time at the bottom of the branchial sac near the esophagus or within the esophagus but make periodic trips into the stomach to deposit their ovisacs (Gotto 1957, 1961).

In compound ascidians, female Notodelphyidae can be found in the branchial baskets or postabdomens of zooids or in the common cloaca of the colony but their most common locus is in the matrix, either free or in cysts formed by the ascidian colony. Males of these notodelphyids are not known. Ascidicolidae in compound ascidians show a wider choice of habitats. They have been found in the branchial basket; stomach; intestine; postabdomen; peribranchial, perivisceral, or epicardial cavities; common cloaca of zooids; or in the common matrix. Both males and females show a considerable peregrination into the matrix (Ooishi and Illg 1977). The paths of movement of ovigerous females are often marked by dropped ovisacs in the matrix or the zooids. Chatton and Harant (1924) described how the ascidicolid *Enterocolides ecaudatus* travelled from deep in the matrix to the surface of the compound ascidian in order to lay its eggs.

The knowledge of the nutritional biology of the ascidicolous copepods is very incomplete. We adopt the neutral term "associate" (Gooding 1957) in referring to these copepods because the trophic nature of the symbiotic association is usually only inferred. For most cases, we would probably be correct in using the term "commensalism" because the interaction is obligate for the associates but no harm appears to devolve to the host. For copepods

living in the branchial baskets, the ascidian appears to supply a nutritional bonanza in the form of plankton or detritus carried in sea water through the branchial siphon and filtered by sheets of mucus on the walls of the branchial basket. The sea water, largely depleted of food, then passes through the modified gill slits (= stigmata) into the atrium and is expelled by the atrial siphon. The sheets of mucus, produced by glands of the endostyle, are moved by cilia along the branchial walls to the dorsal lamina where a more concentrated food string is fashioned and is ultimately passed to the esophagus and stomach. Because of the opacity of most ascidian hosts, it has been difficult to study the behavior of ascidicolous copepods *in situ*, but Gotto (1957, 1979) succeeded in observing the feeding process of female *Ascidicola rosea* living in transparent *Corella parallelogramma*, and female *Pachypygus gibber* living in transparent *Ciona intestinalis*. He found that both females attach to the food string as it passes from the dorsal lamina into the esophagus and feed on particles from the concentrated string. He referred to this mode of feeding as "larder feeding" and suggested that species of *Notodelphys* possibly feed in a somewhat similar manner, although their agility might permit them to nibble on the food captured by the moving mucous sheets on the branchial walls rather than having to attach to the food string.

Species of ascidicolid copepods that occupy the intestine, stomach, or atrium of their hosts would be bathed in partially digested food or feces and might fit Gotto's (1979) category of "debris feeders." The notodelphyid *Scolecodes huntsmani* is known to contain only ascidian blood cells in its gut (Dudley 1968) and, for this grade of interaction, "parasitism" would be more appropriate description than "commensalism." Nothing is known about the actual food or feeding methods of the copepods that live in the tunic of solitary ascidians or in the postabdomen or matrix of compound ascidians.

Ascidicolous cyclopoids are not the only copepods known to be associated with ascidians. In the literature on Copepoda of the world, there are many cases of association of copepods of the order Poecilostomatoida, family Lichomolgidae, with a long roster of ascidian hosts (Humes and Stock 1973) and a single species, *Henicoxiphium redactum* Illg and Humes (1971), has been described from Florida and North Carolina. In our experience, members of the order Harpacticoida are also frequently encountered in association with ascidians, but it is not certain whether there are true symbiotic relationships. Recorded as associates of species of compound ascidians of the genus *Amaroucium* (now *Aplidium*) in the vicinity of Woods Hole, Massachusetts (Seiwell 1928; Wilson 1932; Coull 1977) are the harpacticoids, *Tisbe gracilis* (Scott) (Synonym: *Tisbe wilsoni* Seiwell, 1928) and *Paramphiascella commensalis* (Seiwell), 1928. Because of the many microhabitats within an ascidian, one can also find a rich variety of other organisms living in or on these animals. These other associates include algae, protozoans, hydroid coelenterates, flatworms, nemertean worms, nematode worms, polychaete annelids, burrowing and nestling bivalve molluscs, and crustacean arthropods such as amphipods and decapods. Little is known about the ecology of this microcosm, but predator-prey and competitive interactions and the partitioning of food resources must be very complex.

Life Cycles

Although nothing is known of the development of the Archinotodelphyidae, we have considerable information on the life cycles of some copepods of the family Notodelphyidae (Canu 1892; Dudley 1966; Hipeau-Jacquotte 1978a) and some of the subfamilies of the Ascidicolidae (Canu 1892; Gotto 1957; Dudley 1966; Anderson and Rossiter 1969; Illg and Dudley 1980; Ooishi 1980). These investigators have used cultures in sea water to determine that the life cycle incorporates early free-swimming lecithotrophic naupliar and copepodid stages in both the notodelphyids and the ascidicolids. Only the last few copepodid stages are symbiotic and these have been discovered by careful examinations of ascidians. It is important to emphasize that, because the free stages are lecithotrophic and do not feed during this free existence, they really have an ultimate nutritional dependency on the host.

The nauplii have their antennules, antennae, and mandibles developed as swimming appendages with no feeding functions. Characteristically, the development of the postmandibular appendages is cryptic in nauplii, and only the distal margins of these internally developing appendages are evident on the naupliar exuviae. The yolk in the developing gut of the nauplius, upon which it subsists, is usually brightly colored in shades of red, yellow, green, blue or purple, or mixtures of these, although in some species the yolk is white. Contrasting color patches or spots of orange, yellow, red, brown, or green pigment are often bilaterally arranged in the naupliar body. A single naupliar eye, not always present, is medially placed near the anterior end and ranges from a brilliant red to pink to white. Tapetal crystals impart a shiny appearance to the eye. After a number of naupliar stadia ranging from as few as one, as in *Haplostomella australiensis* (Anderson and Rossiter 1969), to three in some ascidicolids of the Haplostominae (Ooishi 1980), to four in *Ascidicola rosea* (Gotto 1957), to five in most notodelphyids (Dudley 1966) and other Haplostominae (Ooishi 1980), to six in the notodelphyid *Pachypygus gibber* (Hipeau-Jacquotte 1978a), a molt to the first copepodid stage occurs. The number of naupliar stadia and the total length of the naupliar period is dependent not only on the species but is often temperature dependent as well in Notodelphyidae (Dudley 1966; Dudley, unpubl. observ.). In addition, if the embryos have a particularly long incubation time in the female's broodpouch, there may be a smaller number of free-swimming stages after they hatch.

The first copepodids, indeterminable to gender, have a cyclopoid body form with all of the appendages of the cephalosome characteristic of the species present in at least rudimentary form, a metasome of two or three segments bearing swimming legs that are not yet of the definitive form, and a urosome whose most anterior segment bears the rudiments of legs. These copepodids swim actively. At the molt to the second copepodid stage, the exopodite of the antenna is lost in all of the species of ascidicolous copepods studied and other reductions can occur if these are characteristic of the adult of the species. The second copepodid is the infective stage in all notodelphyids studied (Dudley 1966, 1969; Hipeau-Jacquotte 1978a, 1984), becoming photonegative and sinking in the water to enter a benthic ascidian. A similar situation obtains in the ascidicolid haplostomins whose development is known (Ooishi 1980). In notodelphyid second copepodids, proportionately large aesthetes on the antennules and a cephalic sensory organ that reaches its maximal development at this stage and later declines (Dudley 1972), may help in sensing an appropriate host. In the symbiotic stages, with each subsequent molt, legs and cephalosomic appendages progress in their development toward the definitive form of the adult: there are additions of new legs posteriorly up to the characteristic number and a refinement of the segmentation and setation of other appendages. Thus, among copepods extracted from ascidians there is a fair possibility of encountering developmental stages, from the second through fifth copepodids, as well as the adults. In the least modified species, sexual dimorphism is first apparent in the fifth copepodid stages, but, in those species in which sexual dimorphism is profound, the divergence in form between males and females may be more gradual, appearing first in the fourth copepodids.

Male Dimorphism

Two types of males have been reported in the notodelphyids *Doropygus seclusus* from the U.S. Pacific coast (Dudley 1966), *Doropygus laticornis* from the U.S. Atlantic coast (Dudley 1986), and the European *Pachypygus gibber* (Hipeau-Jacquotte 1978 b and c; 1980 a and b; 1984; 1988). These two types of males are referred to as "anamorphic" and "metamorphic" by Dudley and as "typical" and "atypical", respectively, by Hipeau-Jacquotte.

In these notodelphyids, some male fifth copepodids molt to anamorphic (typical) adult males (Fig. 2G), which like the adult females are adapted for life within ascidian hosts. Their cephalosomic appendages are like those of the females; the body segments show fusions; the setae on the appendages are short; and the legs are not adapted for swimming. In *Doropygus* spp., these males move by creeping on the branchial and/or peribranchial wall of the ascidian.

Other male fifth copepodids undergo a profound metamorphosis to become actively free-swimming metamorphic (atypical) adult males with such extreme reductions in the gnathal portions of their mouthparts that it is unlikely that they can feed. However, the augmentation of the setation of their antennules and swimming legs and the streamlining and more functional articulations of the segments of their bodies than in the anamorphic males, makes the metamorphic males very proficient swimmers.

Before the occurrence of such metamorphic males was appreciated, some males collected in the absence of female ascidicoles were diagnosed as notodelphyids, and a genus *Agnathaner* was erected for the reception of such males (Canu 1891). This genus has received a number of species, none pertinent to the fauna of our considerations, but in the main they have been reallocated as the corresponding females have been determined.

With the exception of two males found inside the branchial basket of ascidians, Dudley (1966, 1986) has only obtained the metamorphic males in species of *Doropygus* when their male fifth copepodids were removed from the ascidian and studied in cultures. The anamorphic males are common inhabitants of the host ascidians. Based on results of infection experiments, Hipeau-Jacquotte (1984, 1988) proposed that environmental factors exert an epigenetic effect on the development of the two kinds of males in *Pachypygus gibber*. She has shown (1988) that the development of atypical swimming males in *P. gibber* occurs only within very young representatives of the host *Ciona intestinalis* which she infected with third copepodids of *Pachypygus*. Conversely, the development of typical (anamorphic) males occurs only in older hosts. The causative environmental factors for the development of the typical males appear to be the presence of a female and a sufficient amount of food in the older ascidian hosts, while the reduced amount of food in very young *Ciona intestinalis* evokes the development of atypical swimming males. After the terminal molt of the atypical fifth copepodid within the young ascidian, the atypical swimming male of *Pachypygus gibber* leaves the small ascidian, within which a female cannot develop, and enters into the second pelagic phase in its life cycle. In order to search out a host containing a mature female, the swimming male would undoubtedly require chemical signals and would need effective sensory organs to receive these. Hipeau-Jacquotte (1984, 1986, 1987) has described sensory/glandular complexes, hundreds of which are present on the ventrolateral, pleural surfaces of the cephalosome of atypical swimming males, but absent in the typical males and females. Each functional unit, possibly chemosensory, consists of 2 bipolar sensory cells whose dendrites have basal 9 + 0 cilia, 1 envelope cell, and 1 apical cell which forms a canal through the cuticle. The long dendrites from the sensory cells pass through the cuticular canals and are exposed externally on the margins of the cephalosome. These long end organs lack a cuticular covering and become paraciliary distally, containing hundreds of microtubules. Secretions from

adjacent exocrine dermal glands are released through pores and spread over the cephalosomic cuticle and the sensory dendrites (Hipeau-Jacquotte 1987). These secretions, according to this author, may serve to amplify transduction by absorbing chemostimulatory compounds or they may serve a protective function for the long, naked dendritic processes. Gotto et al. (1984), using SEM, have described structures which project from the lateral surfaces of the cephalosome in the swimming males of the enteropsin *Mychophilus roseus* that appear to correspond to the external dendrites in *P. gibber*. Nishida (1986), using both TEM and SEM, has also described similar presumable sensory organs on cephalosomes of males of free-living planktonic species of *Oithona*, thus showing that they are not exclusive to swimming males of ascidicolous cyclopoids.

Hipeau-Jacquotte (1989) has also shown that spermatogenesis, when nonflagellate, but motile spermatozoa are formed and encased in spermatophores are formed, is identical in the atypical and typical males of *Pachypygus gibber*. Both males can mate with mature females, using their prehensile antennae to hold onto the females' appendages in slightly different ways, and can attach spermatophores to the females' gonopore. The atypical male, at least under the culture conditions used, dies after extruding only one spermatophore from each of its two gonopores because the process destroys its genital segment. The typical males, however, can discharge at least two sets of two spermatophores and maybe more.

All of the other species of notodelphyids and ascidicolids in which males are known have only one kind of male, either a creeping male or, more commonly, a swimming male (Dudley 1966, 1986; Ooishi and Illg 1977, 1986). Creeping males in some species of notodelphyids, found only in the ascidians, have appendages that are similiar to those of the females. Swimming males in notodelphyids may be one of two types: 1) males of the least modified species (for example, those in *Notodelphys* spp. that are about 1/2 to 2/3 the lengths of the females, are very active, can swim, can commonly be found in the ascidians, and have appendages that are very similar to those of the females and probably feed in the same way) and 2) males of greatly modified notodelphyid species such as those of *Gunenotophorus* and *Scolecodes* spp. that are very much smaller than the females and have appendages that are very different. These males show losses of gnathal portions of the mouthparts and attenuation of the residual components and probably are unable to feed in the same ways as their corresponding females. In the Ascidicolidae, there is less difference in the appendicular structure of creeping and swimming males in the various species of *Haplostoma*. Both males show modifications in their mouthparts which are reminiscent of the changes shown by type-2 swimming males of the notodelphyids (Ooishi and Illg 1977). Similar modifications are seen in all other swimming males in the Ascidicolidae, with the possible exception of the male of *Ascidicola rosea*, which has mouthparts like those of the females (Monniot 1965) and is, therefore, more like type-1 swimming males in the notodelphyids.

Materials and Methods

Collections of Ascidian Hosts

The problems of collecting ascidicolous copepods are in the main those of obtaining quantities of ascidians, the host organisms. These are entirely marine, very few tolerating even an approach to brackish conditions. Availability of free-flowing water is a prime requisite for abundance of ascidians, notable encrusting organisms of piers and floats. However, our experience indicates that the most favorable source for infested ascidians would be bottom-dwelling beds, usually below the level of tidal fluctuation. Dredging or SCUBA operations, therefore, offer the recommended procedures for collecting the hosts. Our experience in dealing with the various developmental stages of copepods has demonstrated a very striking reversal of phototactic locomotion as the copepods reach the infesting stages and seek the hosts. This situation, of course, explains the predominance of successful infestations in bottom-dwelling hosts.

Assisted by colleagues and the staff of the Systematics-Ecology Program, Marine Biological Laboratory at Woods Hole, we dredged from the SS *Verrill*, collected specimens from Boston whalers in waters of the Cape Cod region, collected specimens in the intertidal zone in Maine, and were able to obtain most of the live ascidians used as hosts in this study. We also had access to preserved ascidian species from USFW expeditions to the Gulf of Maine and from the Gray Museum of the Marine Biological Laboratory. Ascidians from this northeastern region represent both the Atlantic boreal population north of the Cape and in its deep outer banks and the Atlantic temperate population south of the Cape, as well as cosmopolitan species (Van Name 1945; Plough 1978). We also made intertidal collections in Florida, assisted by the staff of the Smithsonian Marine Station at Link Port, Fort Pierce, FL and were, therefore, able to sample ascidians from the West Indian Region (Van Name 1945; Plough 1978). Collections of the National Museum of Natural History, Smithsonian Institution, and the American Museum of Natural History were drawn upon for confirmatory specimens of previously recorded collections and for additional specimens extracted by us from identified ascidians in their collections. We did not collect live specimens from localities north of Maine or south of Fort Pierce, FL but we have expanded our list with copepods we extracted from preserved ascidians and with the meager published records of material from along the Atlantic Coast of North America from Labrador to Key Biscayne, FL, which we corroborated wherever possible by examination of voucher specimens of the

copepods. Of the 25 species of preserved or newly collected ascidians examined by us, representatives of 11 species were found to possess copepod associates. An additional roster of 7 ascidian host species is based on earlier published reports. The publications consulted were those of Blake (1929, 1933), Gray (1938), Illg (1955, 1958), Pearse (1947), Préfontaine (1936), Préfontaine and Brunel (1962), and Wilson (1921, 1932).

The following tables present, alphabetically, new records of associations (Table 1) and the confirmed and unconfirmed reports from the literature (Table 2).

Methods of Obtaining and Studying Copepods

Relatively few copepods inhabit compound ascidians of our region; so far finds have been made only in association with species of *Aplidium* (= *Amaroucium*). The few that so occur are sometimes observable in the living host but a serious

Table 1

New records from eastern North America of ascidian hosts and their associated symbiotic copepods of the families Ascidicolidae and Notodelphyidae. Names of ascidian species follow Van Name (1945).

Ascidian host	Copepod associates
Aplidium glabrum (Verrill)	*Botryllophilus* sp. *Haplosaccus elongatus* Ooishi and Illg
Ascidia callosa Stimpson	*Buprorus loveni* Thorell *Schizoproctus inflatus* Aurivillius
Ascidia curvata (Traustedt)	*Notodelphys monoseta* Pearse
Ascidia obliqua Alder	*Buprorus loveni* Thorell *Doropygopsis longicauda* (Aurivillius)
Ascidia prunum Müller	*Buprorus loveni* Thorell
Boltenia echinata (Linnaeus)	*Doropygus demissus* Aurivillius
Boltenia ovifera (Linnaeus)	*Schizoproctus inflatus* Aurivillius
Molgula arenata Stimpson	*Doropygus laticornis* Wilson
Styela partita (Stimpson)	*Botryllophilus norvegicus* Schellenberg

Table 2

Published records from eastern North America of ascidian hosts and their associated symbiotic copepods of the families Archinotodelphyidae, Ascidicolidae and Notodelphyidae. Names of ascidian species follow Van Name (1945).

Ascidian host	Copepod associate	References
Confirmed published records		
Aplidium glabrum (Verrill)	*Haplostomides amarouci* (Blake)[a]	Blake 1929
Ascidia callosa Stimpson	*Doropygopsis longicauda* (Aurivillius)[a]	Blake 1933
Ascidia interrupta Heller	*Notodelphys monoseta* Pearse[b]	Pearse 1947; Illg 1958
Ascidia prunum Müller	*Doropygus demissus* Aurivillius[b]	Illg 1958
	Doropygopsis longicauda (Aurivillius)[a, b]	Illg 1958
Boltenia ovifera (Linnaeus)	*Doropygus demissus* Aurivillius[a, b]	Illg 1958; Préfontaine and Brunel 1962
"Cynthia carnea" Verrill = *Dendrodoa carnea* (Agassiz) 1932 or *Styela coriacea* (Alder and Hancock)	*Botryllophilus norvegicus* Schellenberg[b]	Wilson 1921, 1932
Molgula complanata Alder and Hancock	*Doropygus pulex* Thorell[b]	Wilson 1932
Molgula manhattensis DeKay	*Doropygus laticornis* Wilson[a, b]	Wilson 1932
Styela coriacea (Alder and Hancock)	*Gunenotophorus curvipes* Illg[a, b]	Illg 1958
Styela partita (Stimpson)	*Doropygus curvatus* Gray[a]	Gray 1938
	Pararchinotodelphys gurneyi Illg[a, b]	Illg 1955
Styela plicata Lesueur	*Doropygus pulex* Thorell[b]	Illg 1958
	Pachypygus macer Illg[a, b]	Illg 1958
Unconfirmed published records		
Ascidia callosa Stimpson	*Botryllophilus* sp.	Blake 1933
Ascidia obliqua Alder	*Botryllophilus* sp.	Wilson 1932
Corella parallelogramma Müller	*Notodelphys agilis* Thorell	Wilson 1932
Didemnum albidum (Verrill)	*Haplostomides amarouci* (Blake)	Blake 1929
Polycarpa fibrosa (Stimpson)	*Botryllophilus norvegicus* Schellenberg	Préfontaine 1936; Préfontaine and Brunel 1962
Styela mollis (Stimpson)	*Botryllophilus norvegicus* Schellenberg	Préfontaine 1936; Préfontaine and Brunel 1962

[a] New collections confirm reported occurrences.
[b] Verification of identity based on examinations of voucher copepod specimens.

canvass for associated copepods would require processing the ascidians. Teasing out zooids is necessary for capture of forms in branchial cavities. Sometimes hosts left in stale water will extrude the zooids, or the stagnation effects may induce copepods of some motility to leave the host. The most favorable procedure involves systematic slicing and teasing of the colony to expose associates embedded in the matrix and inhabiting the zooids or associated channels and cavities in the matrix.

The majority of forms will be found within the bodies of simple, or solitary, ascidians. These may be tumbled out by wholesale slicing of quantities of ascidians. Preferably, a systematic search may be made by dissection of the host, which procedure assures the preservation of the ascidian specimen for taxonomic identification or voucher preservation and yields the optimum in details of biological relationships of host and associated copepod. For dissection, it is necessary to orient the ascidian. If the siphons are obvious, the tunic may be slit well away from them and peeled like a rind from the enclosed body. If there is no surface landmark for orientation, the best procedure is cautious peeling to expose the body and establish the location of the siphons. The exposed body should then be oriented and the dissection commenced by cutting off the siphons. The body may then be opened by a cut between the siphons, this proceeding ventrally along one side of the body so that the latter can be opened like a book. Alternatively, the body can be sectioned by a deep cut around the whole periphery just to one side of the midline and proceeding from one siphon around to the other, leaving the two halves of the body united by the intersiphonal portion. In individuals with thin or transparent tests this procedure can be accomplished by cutting directly through test and all. The sectioned body can be spread open and pinned down, preferably under water. Conspicuous commensals will often be detected lying in the branchial cavity. A more thorough search, preferably under magnification, should proceed by exploring the plications and other recesses of the branchial basket or pharynx. The branchial basket should then be separated from the mantle by lifting it at the edges and by severing the many small vascular connecting strands. Care should be taken to avoid undue damage to these. The gut and gonads will be among the organs exposed in the epicardial cavity. The wall of the stomach should be slit and the lumen investigated for copepods. Adult males, developmental stages, and, rarely, females may be found in the atrial cavity clinging to the atrial side of the branchial wall.

Living copepods may be placed in 15 to 25 mL of sea water in embryologically clean covered Stender dishes which should be maintained at about normal seawater temperature. Gravid females so maintained often release nauplii which can be further studied to establish the sequence of developmental stages. Unfiltered seawater of reasonable quality is adequate for such maintenance of the organisms. Contact of the seawater with metals such as copper, aluminum, and zinc should be avoided. The procedure might be referred to as "culturing" in the sense that clean dishes and daily or more frequent changes of water should be maintained. No specially prepared medium is required because the naupliar stages lack a patent gut and subsist on their abundant yolk. Study of such developmental stages can proceed by maintaining large numbers in culture dishes, which should be examined regularly for the detection of exuviae. Alternatively, a single nauplius may be maintained and the exuviae collected *en masse* after the last stage attainable in culture has been reached. Such collected exuviae should be mounted directly in glycerine and maintained or studied immediately as wet mounts in seawater on slides. Microscopic examination of living nauplii, using drop slides or other pressure-protected mounts, will reveal the development of the postmandibular appendages.

Adult individuals are readily fixed and preserved by the standard fixatives and preservatives. Very contractile specimens may be induced to die in a relaxed state by floating a drop or two of clove oil in a small amount of water in which they are contained. Direct fixation in 95% ethanol is satisfactory, as is fixation in dilute formalin, Bouin's fixative, Helly's mixture or other combinations. Transfer to 70% ethanol, preferably containing a small amount of glycerine, is suitable for long-range storage of the specimens.

For taxonomic determination it is necessary to prepare microscopic slide mounts of the copepods. For best preservation on slides, we have found green-tinted Euparal to be the best mountant. Dissection of the copepod in this medium with fine needles requires some practice, however, because the solvent Euparal Essence must constantly be added to keep the mountant fluid. Temporary slide mounts can be readily made in glycerine or lactic acid, preferably tinged lightly with Methyl Blue, Lignin Pink, Chlorazol Black or other appropriate stain. Dissection is greatly facilitated by softening the copepod in a drop or two of tinted lactic acid. A few minutes will usually prepare the specimen for dissection which may then be carried on under magnification with fine-tipped needles. Such dissections can be studied directly in the dissecting medium, or a slightly longer lasting preparation can be prepared by transferring the appendages dissected in lactic acid to polyvinyl lactophenol or to various media for mounting insects, such as Faure's, Reyne's and Hoyer's formulae. Mounts in the latter media can be made somewhat longer lasting by ringing with cements such as Murrayite or with transparent fingernail polish. Pressure-protected and nondistorted mounts should of course be sought for purposes of adequate study and taxonomic determination. A detailed account of methods of anatomical preparation is presented in a paper by Humes and Gooding (1964).

Key to the Copepoda, Cyclopoida: Archinotodelphyidae, Notodelphyidae, and Ascidiocolidae of the Eastern United States

1 Body of typical cylopoid form (Fig. 1, A through E) (*see* description p. 5) ..... ***Pararchinotodelphys gurneyi***

1 Body not of typical cyclopoid form; modified in some appreciable way as by formation of internal broodpouch or fusion of body segments (Figs. 2, A through E; 5, A through F; 8; 9) **2**

2(1) Mature female with internal broodpouch, enclosed dorsally and laterally within one or more thoracic segments (Figs. 2, A through E; 5A; 8; 9) **3**

2(1) Mature female lacking internal broodpouch but possessing external ovisacs dependent from genital segment at times of reproduction (Fig. 5, C, E, and F) **13**

3(2) Antenna (= second antenna) uniramous, bearing one terminal articulated prehensile hook and up to 6 short setae on apical margin of distal segment (Figs. 6, 18, 19) **4**

Figure 6
Antenna, *Doropygus curvatus*.

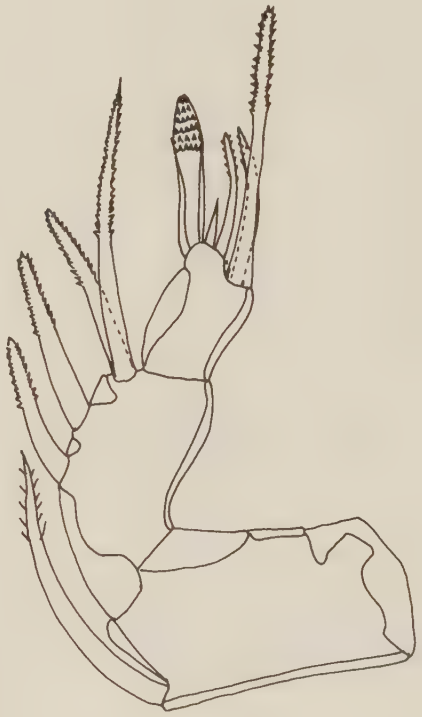


Figure 7
Antenna, *Buprorus loveni*.

3(2) Antenna (= second antenna) uniramous, lacking articulated, prehensile hook, but with 5 stiffened setae on apical margin of distal segment (Fig. 7) ..... ***Buprorus loveni*** **(Fig. 5A)**

4(3) Body dorsoventrally depressed; broodpouch in thoracic segments of 4th and 5th legs bulging dorsally and laterally; urosome continuing straight from forebody (Figs. 8, 2A) 5

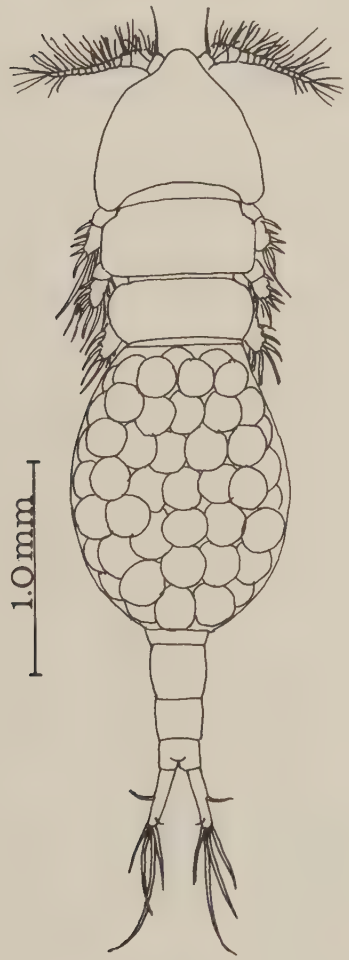


Figure 8
Notodelphys agilis female, dorsal view.

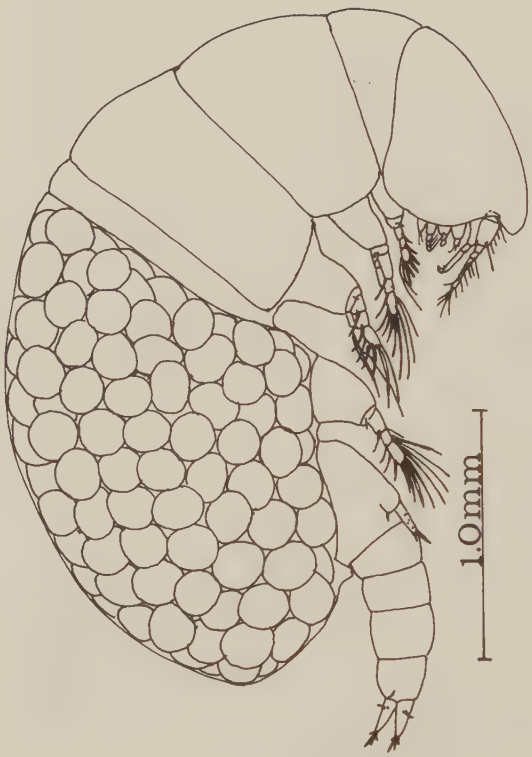


Figure 9
Doropygus curvatus female, lateral view.

4(3) Body laterally compressed; broodpouch in one or more thoracic segments bulging laterally and dorsally; body curved, urosome held at angle to forebody (Figs. 9; 2, B through E) 6

5(4) Terminal segment of fifth leg with a seta and a spine (Fig. 10). Lateral seta set at approximate middle of caudal ramus (Fig. 12) ..... ***Notodelphys agilis* (Fig. 8)**

Figure 10
Fifth leg, *Notodelphys agilis*.

Figure 11
Fifth leg, *Notodelphys monoseta*.

Figure 12
Anal segment and caudal rami, *Notodelphys agilis*.

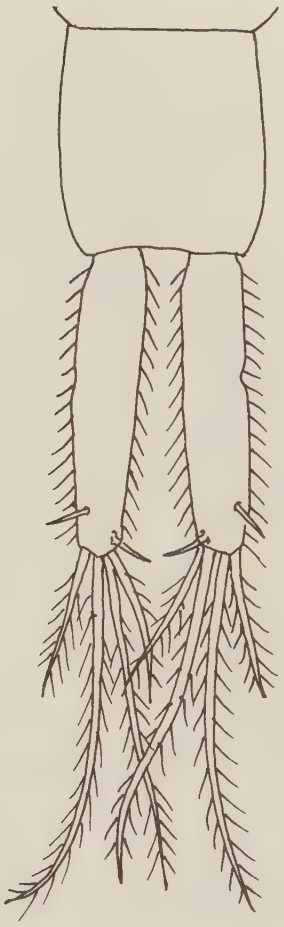


Figure 13
Anal segment and caudal rami, *Notodelphys monoseta*.

5(4) Terminal segment of fifth leg with single seta (Fig. 11). Lateral seta set at approximate distal fifth of caudal ramus (Fig. 13) ..... ***Notodelphys monoseta*** **(Fig. 2A)**

6(4) Broodpouch occupying mainly thoracic segment of fourth legs (= fifth thoracic segment). Body segments anterior to fifth thoracic segment not markedly inflated (Figs. 2, B through D; 9). Rami of all legs straight, setiferous (Fig. 4, A through C) 7

6(4) Broodpouch occupying segments of second through fourth legs (= third through fifth thoracic segments). Body segments anterior to fifth thoracic segment markedly inflated (Fig. 2E). Rami of legs 2–4 curved, sprawling apart. Exopodites and endopodites of legs 2–4 contorted and lacking normal setiform and spiniform armature ..... ***Gunenotophorus curvipes*** **(Fig. 2E)**

7(6) Maxilliped slender, of 3 segments; basal segment longest with 8 or 9 setae; second segment with single long seta; apical segment a truncated cone with 4 setae (Figs. 14, 15) 8

Figure 14
Maxilliped, *Doropygopsis longicauda*.

Figure 15
Maxilliped, *Pachypygus macer*.

7(6) Maxilliped flattened, squat, basically of 2 segments; basal segment bearing 9 setae; apical segment very small, bearing 2 plumose setae (Fig. 16); apical segment sometimes only obscurely articulated with basal segment (Fig. 17) 9

Figure 16
Maxilliped, *Doropygus demissus*.

Figure 17
Maxilliped, *Doropygus curvatus*.

8(7) Distalmost seta of maxilliped long and plumose (Fig. 14); antenna with basal segment bearing one long, plumose seta and one very short seta (Fig. 18) ..... ***Doropygopsis longicauda*** **(Fig. 2B)**

Figure 18
Antenna, *Doropygopsis longicauda*.

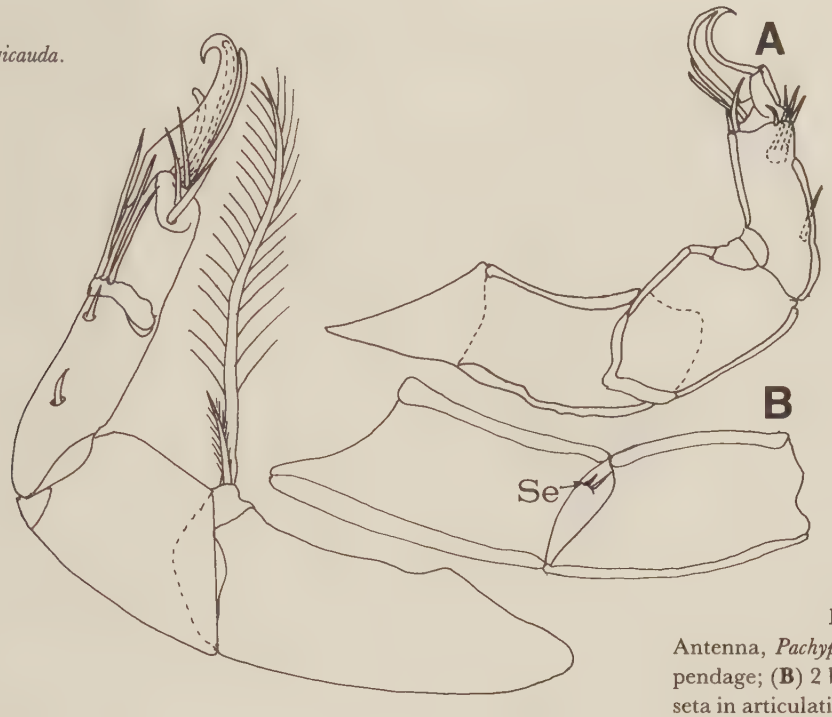
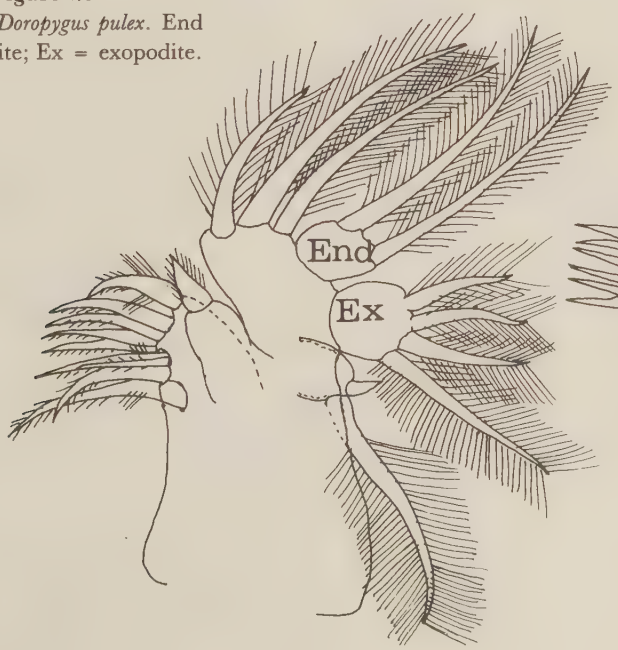


Figure 19
Antenna, *Pachypygus macer*; (**A**) entire appendage; (**B**) 2 basal segments with small seta in articulative membrane. Se = seta.

8(7) Distalmost seta of maxilliped very short (Fig. 15); antenna with basal segment lacking setae (Fig. 19A) or with one or two very minute setae on articulative membrane between basal and second segments (Fig. 19B) ..... ***Pachypygus macer*** **(Fig. 2D)**

9(7) Maxillular endopodite with 2 setae (Figs. 20, 21) **10**

Figure 20
Maxillule, *Doropygus pulex*. End = endopodite; Ex = exopodite.



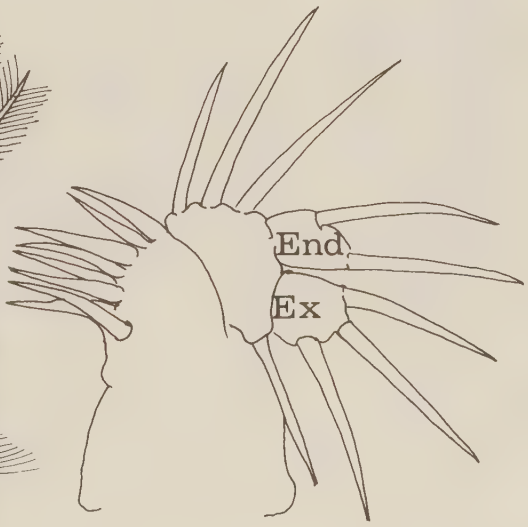


Figure 21
Maxillule, *Doropygus schellenbergi*. End = endopodite; Ex = exopodite.

9(7) Maxillular endopodite with 3 setae (Figs. 22, 23) 11

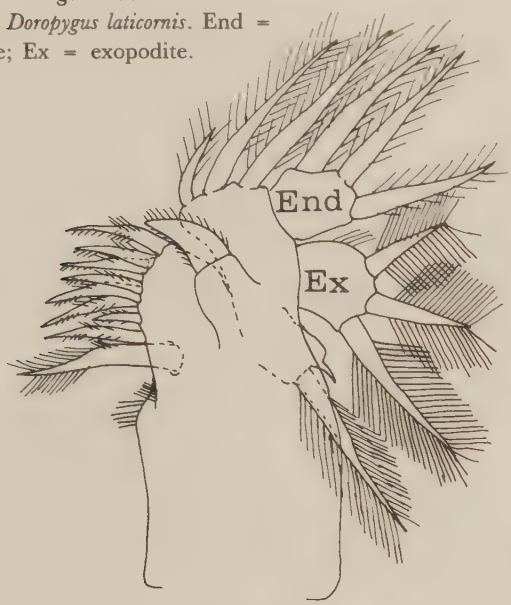


Figure 22
Maxillule, *Doropygus laticornis*. End = endopodite; Ex = exopodite.

Figure 23
Maxillule, *Doropygus curvatus*. End = endopodite; Ex = exopodite.

10(9) Maxillular exopodite with 4 setae (Fig. 20) ..... ***Doropygus pulex***

10(9) Maxillular exopodite with 3 setae (Fig. 21) ..... ***Doropygus schellenbergi***

11(9) Mandibular exopodite with 4 setae (Fig. 24) ..... ***Doropygus laticornis*** **(Fig. 2C)**

Figure 24
Mandible, *Doropygus laticornis*. Ex = exopodite.

Figure 25
Mandible, *Doropygus curvatus*. Ex = exopodite.

11(9) Mandibular exopodite with 5 setae (Fig. 25) 12

12(11) Maxilliped clearly 2-segmented; distal segment bearing 2 setae and clearly articulated with basal segment (Fig. 16) ..... ***Doropygus demissus***

12(11) Maxilliped with distal segment indicated only as lobe bearing 2 setae; no clear articulation with basal segment (Fig. 17) ..... ***Doropygus curvatus* (Fig. 9)**

13(2) Legs 1–4 biramous, each with 1-segmented exopodite and endopodite (Figs. 26, 28) or with 1-segmented exopodite and obscurely 2-segmented endopodite (Fig. 27); caudal rami with apical, prehensile, hooked claws (Figs. 29, 30) 14

Figure 26
Right first leg, *Botryllophilus* sp. from *Aplidium glabrum*. End = endopodite.

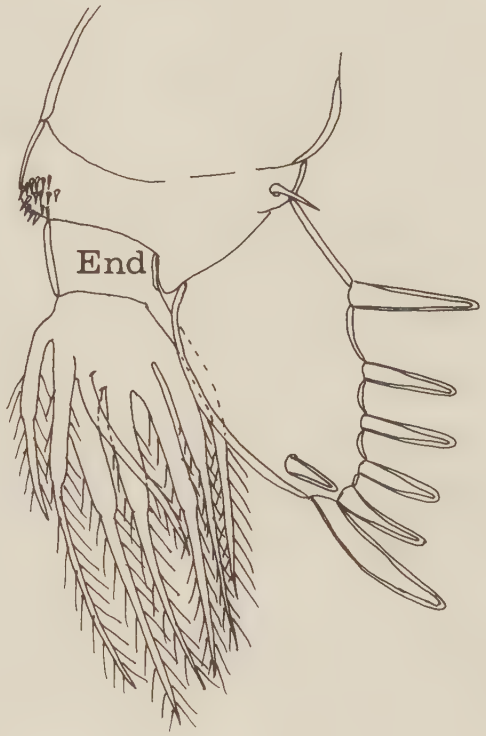


Figure 27
Right first leg, *Botryllophilus norvegicus*. End = endopodite.

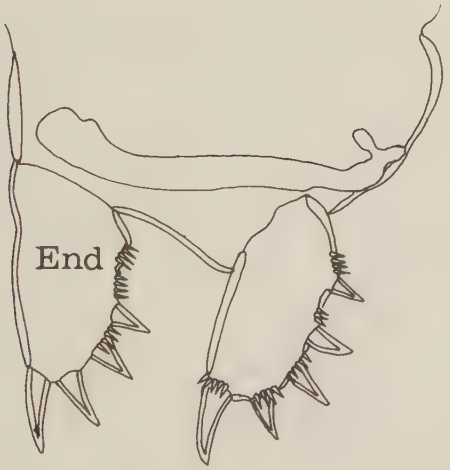


Figure 28
First leg, *Schizoproctus inflatus*. End = endopodite.

Figure 29
Caudal ramus, *Botryllophilus* sp. from *Aplidium glabrum*.

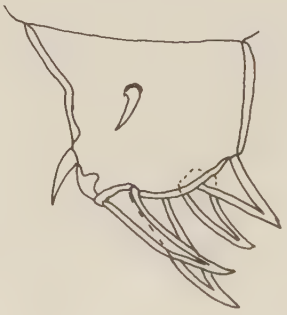


Figure 30
Caudal ramus, *Schizoproctus inflatus*.

13(2) Legs 1–4 uniramous; single ramus (exopodite) of one segment, not clearly articulated with protopodite (Figs. 31, 32); caudal rami without prehensile claws, armed only with setiform or spiniform elements (Figs. 33, 34) 16

Figure 31
First leg, *Haplostomides amarouci*.

Figure 32
First leg, *Haplosaccus elongatus*.

Figure 33
Caudal ramus, *Haplostomides amarouci*.

Figure 34
Caudal ramus, *Haplosaccus elongatus*.

14(13) Fifth legs lamellate (Fig. 35); endopodites of legs 1–4 armed only with spines (Figs. 36, 28) ..... ***Schizoproctus inflatus*** **(Fig. 5D)**

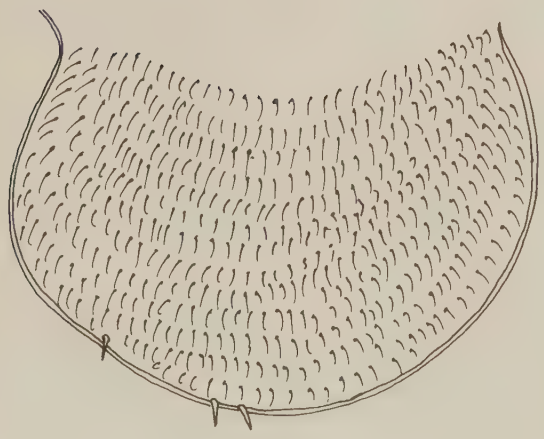


Figure 35
Fifth leg, *Schizoproctus inflatus*.

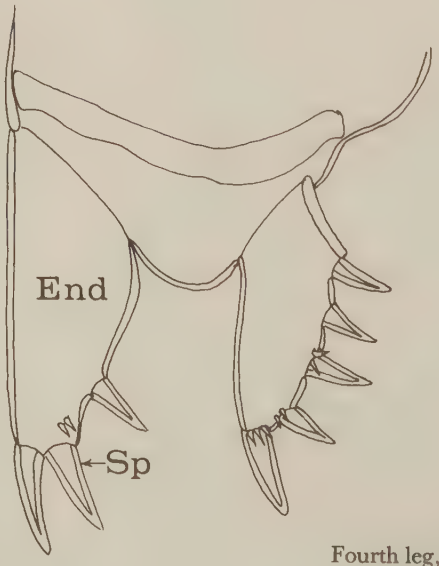


Figure 36
Fourth leg, *Schizoproctus inflatus*. End = endopodite; Sp = spine.

14(13) Fifth legs not lamellate, otherwise (Figs. 37, 38); endopodites of legs 1–4 armed with setae (Figs. 39, 26, 27) **15**

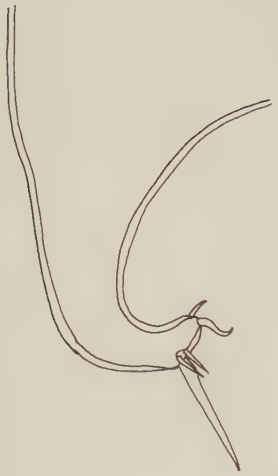


Figure 37
Fifth leg, *Botryllophilus norvegicus*.

Figure 38
Fifth leg, *Botryllophilus* sp. from *Aplidium glabrum*.

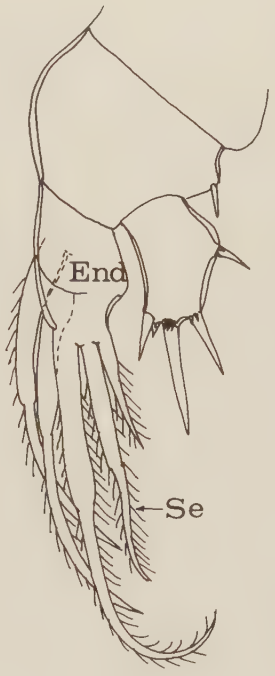


Figure 39
Right fourth leg, *Botryllophilus* sp. from *Aplidium glabrum*. End = endopodite; Se = seta.

15(14) Distal segment of antenna with 5 spiniform elements of armature (Fig. 40) ..... ***Botryllophilus norvegicus*** **(Fig. 5B)**

15(14) Distal segment of antenna with 7 setiform elements of armature (Fig. 41) .... ***Botryllophilus*** **sp. (Fig. 5C)**

Figure 40
Right antenna, *Botryllophilus norvegicus*.

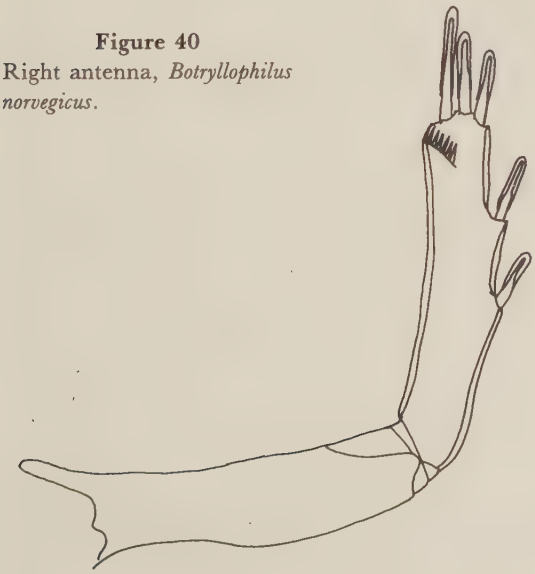


Figure 41
Right antenna, *Botryllophilus* sp. from *Aplidium glabrum*.

16(13) Mandibles, maxillules and maxillae reduced; all setiferous (Figs. 42 through 45) .....
..... *Haplostomides amarouci* **(Fig. 5E)**

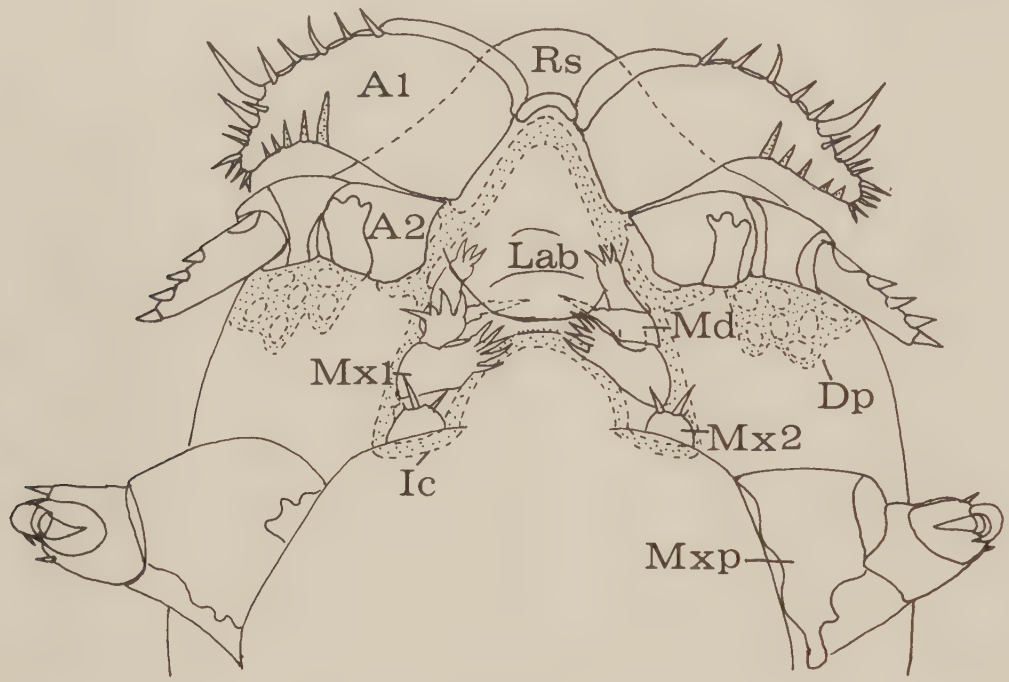


Figure 42
Appendages of cephalosome, *Haplostomides amarouci*, ventral view. A1 = first antenna (antennule); A2 = second antenna (antenna). Dp = dorsal cuticular plate; Ic = internal cuticular support; Lab = labrum; Md = mandible; Mxl = first maxilla (maxillule); Mx2 = second maxilla (maxilla); Mxp = maxilliped; Rs = rostrum.

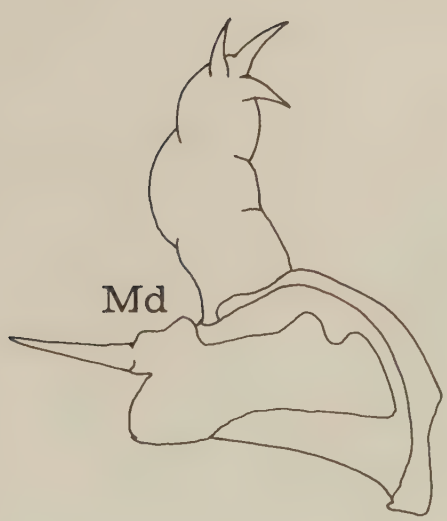


Figure 43
Mandible, Md, *Haplostomides amarouci*.

Figure 44
Maxillule, Mx1, *Haplostomides amarouci*.

Figure 45
Maxilla, Mx2, *Haplostomides amarouci*.

16(13) Mandibles, maxillules and maxillae reduced lobes without normal setae (Figs. 46, 47) .....
..... *Haplosaccus elongatus* **(Fig. 5F)**

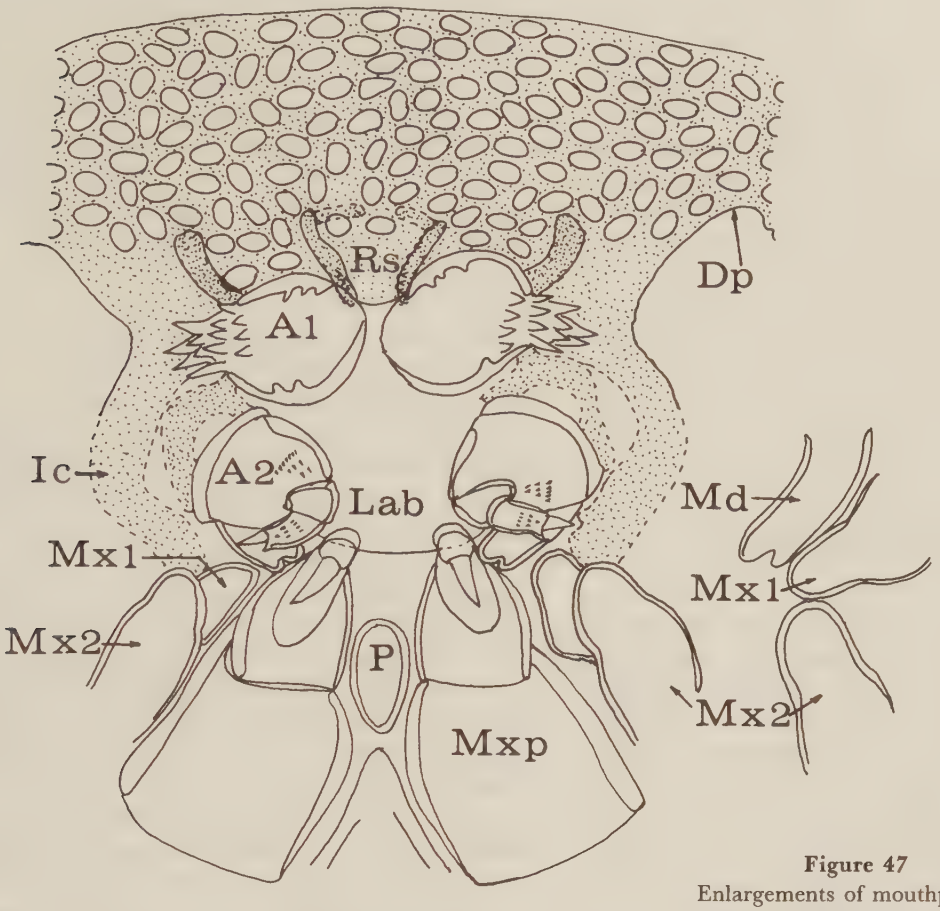


Figure 46
Appendages of cephalosome, *Haplosaccus elongatus*, ventral view. A1 = first antenna (antennule); A2 = second antenna (antenna). Dp = dorsal cuticular plate; Ic = internal cuticular support; Lab = labrum; Mxl = first maxilla (maxillule); Mx2 = second maxilla (maxilla); Mxp = maxilliped; P = post-oral plate; Rs = rostrum.

Figure 47
Enlargements of mouthparts of *Haplosaccus elongatus*. Md = mandible; Mxl = maxillule; Mx2 = maxilla.

Annotated Systematic List

The following list of ascidicolous copepods of the Cyclopoida (17 species) is arranged systematically in families after Illg (1955, 1958) and Illg and Dudley (1980), according to a range of morphological adaptations of the copepods to life in host ascidians. Within the family Notodelphyidae, we list the type genus first and then present the other genera alphabetically. In the genus *Doropygus*, the type species is given first, and the other species follow alphabetically. Subfamilies of the family Ascidicolidae are also in alphabetical order. Data on collections in the area covered here are given as well as an indication of the world distribution of species which are not endemic to the eastern United States. Wherever possible, museum catalog numbers are given for preserved collections. Additional voucher specimens of newly collected material, as seemed appropriate to us, have been deposited in the U.S. National Museum of Natural History, Smithsonian Institution.

Family ARCHINOTODELPHYIDAE Lang, 1949

***Pararchinotodelphys gurneyi* Illg, 1955**—Found in the branchial cavity of a specimen of *Styela partita* (Stimpson), United States National Museum (USNM) No. 3181, collected about 85 miles southeast of Martha's Vineyard, Mass., lat. 39°54′N, long. 69°51′30″W; USFC R/V *Fish Hawk* Sta. 940, 4 Aug. 1881, 134 fathoms[?], black sand; 4 females (Holotype, USNM No. 97608, Paratypes USNM No. 92536). The species was described from preserved specimens (Illg 1955) and has never been seen alive. The inclusion here of this species is tentative. Normally the seaward limit of distribution of forms in the MFFEUS manuals is about 200 m. The record of collection of this species from the continental slope at a depth of 134 fathoms would seem disqualifying. The identification of the host as *Styela partita* introduces a complication. The authority for the identification is not known. The species is cited by Plough (1978) as an inshore, shallow-water species. If the host identification is correct it is possible that *P. gurneyi* will be encountered again in collections from our area. However, the tendency of archinotodelphyid species to inhabit deep waters, as far as records to date would indicate, may be the deciding factor to eliminate the species from the present list.

Family NOTODELPHYIDAE Dana, 1853

***Notodelphys agilis* Thorell, 1859**—Wilson (1932) recorded 3 females from *Ascidia* (now *Corella*) *parallelogramma* Müller at Woods Hole, Mass., 6 fathoms, in 1925. His distribution records also refer to an occurrence at the Bay of Fundy, Maine (USNM 54090). We have examined the latter specimens and determined them to be *Doropygopsis longicauda* (Aurivillius). Illg (1958), with reference to the North American fauna and, particularly concerning published reports of this species at Woods Hole, notes "some of the reported occurrences have been checked and the specimens upon which they were based have been found to be representatives of other species." We have not been able to confirm the occurrence of this species on the North Atlantic coast of North America. Many published records place this species in the European fauna. Thorell (1859) recorded the color of the ova and embryos as "fusco-virentia."

***Notodelphys monoseta* Pearse, 1947**—This was described from *Ascidia interrupta* Heller at Beaufort, North Carolina. Illg (1958) redescribed the species from the type lot. We have made new collections of this species, the only collections made since the original description: 1 female, 1 male, 1 female fifth copepodid from *Ascidia curvata* (Traustedt), on shell, intertidal on −0.8′ tide, Little Jim Island, Indian River, Florida, 3/7/77; 3 females, 1 immature adult female, 1 female fifth copepodid, 1 fourth copepodid from *Ascidia curvata* (Traustedt), on rocks, intertidal on −0.8′ tide, Sebastian Inlet, Indian River, Florida, 3/8/77. According to Van Name (1945), both of the ascidian hosts are southern species. *A. interrupta* ranges from North Carolina to the southern coast of Brazil. *A. curvata* ranges from Florida to West Indies and Puerto Rico.

***Doropygopsis longicauda* (Aurivillius) 1882 (Synonyms: *Doropygus longicauda* Aurivillius, 1882; *Doropygopsis longicauda* Sars, 1921)**—We removed one male from a specimen of *Ascidia obliqua* Alder, an ascidian supplied and identified by H. Plough and collected USFW, *Alb. IV*-64, off Portsmouth, N.H., 43°03′N, 70°24′W., 98 m, 1/17/64. Other specimens examined include 11 females, 3 males and 1 fifth copepodid from *Ascidia prunum* Müller, intertidal, Eastport, Maine, collectors M.P. Morse and N. Riser, 4/26/76. Specimens from *Ascidiopsis complanata* Verrill (now *A. prunum* Müller), identified by C.B. Wilson as *Notodelphys agilis*, from Todd's Head, Bay of Fundy, Maine, 1872, 25–30 fm, have been re-identified by us as the present species. Illg's (1958) records include females from *Ascidia* sp. from off Grand Manan Island, New Brunswick and from the entrance to Goose Bay, Lake Melville, Labrador, one female from *A. prunum* Müller from Lake Melville, Labrador and males and females from unidentified ascidians from off Labrador. Blake (1933) listed both sexes of *Doropygopsis longicauda* as associates of *Ascidia callosa* Stimpson from the Mt. Desert Island region, Maine. This species is circumboreal, reported in *Phallusia* (now *Ascidia*) *obliqua*, *A. callosa* and unidentified species of *Ascidia* from off Sweden, Norway, Iceland, Greenland (Davis Strait) and it is an associate of *A. callosa* and *A. paratropa* (Huntsman)

in the Pacific Ocean off Washington State and British Columbia. Van Name (1945) reported that *A. callosa* is an inhabitant of shallow water to moderate depths, usually found in water shallower than 30 fathoms but occasionally extending as deep as 80 fathoms. It is circumboreal, as is *A. prunum*, but the latter species lives in water from a few fathoms below low water to 100 fathoms, while *A. obliqua* is principally a species of deep water, with American records ranging from 33 to 289 fathoms. While we have not collected any specimens of this copepod in the Cape Cod area, its collection could be expected on the banks off Cape Cod since *A. callosa*, *A. prunum*, and *A. obliqua* all extend there (Van Name 1945; Plough 1978). Because all of the specimens collected for this report were in preserved ascidians, we were unable to verify that the colors of the copepod conform to those of the Pacific specimens. The latter females are whitish, transparent, have a bright red eye and rose-lavender embryos in their broodpouches. The males are colorless and exhibit an agility comparable to those of species of *Notodelphys*.

***Doropygus pulex* Thorell, 1859**—Two females of this species were obtained by Wilson (1932) in a *Molgula papillosa* Verrill (now *M. complanata* Alder and Hancock) dredged in 6 fathoms off Martha's Vineyard on a stony bottom, 25 July 1924. We have confirmed the identification of these as *D. pulex* (USNM 56573) but we have not been able to establish an exact attribution of the host since there is no record of its preservation. As Illg (1958) points out, the recorded distribution of this copepod species is virtually worldwide. This is the most extensive record compiled for any notodelphyid and the roster of its hosts is the most diverse. We have discussed the broad concept applied to this species by previous investigators, our recognition of the degree of variation of representatives from different hosts, and our belief that *D. pulex s. lat.* represents a complex of populations with morphological distinctions correlated with occurrences in particular hosts (Illg and Dudley 1961, 1965). It may be that when the variant populations, including the population in *M. complanata* in the northeastern United States are studied in detail, they may prove to be separate species rather than conspecific. We have proposed that the type host for Thorell's species be fixed as a member of the family Ascidiidae (Illg and Dudley 1961, 1965). Because we have seen no living specimens of this copepod in the Woods Hole region, we have no information on its biology or color. Records of occurrence of this species from *Boltenia ovifera* (Linnaeus) from the St. Lawrence Estuary were published by Préfontaine and Brunel (1962), based on collections made in 1933 by Préfontaine and determined by C.B. Wilson. Another collection from *B. ovifera* of Préfontaine, 1929, identified by Wilson, was re-identified by Illg (1958) as *Doropygus demissus* and so published by Préfontaine and Brunel (1962). Coming from identical hosts, these two occurrences would seem to be conspecific but the material first listed has not been found for verification. We find this host association dubious and thus doubt the record. We have specimens confirming the distribution of this species in the southeastern United States. Illg's (1958) record from ?*Styela plicata* (Lesueur) from Key Biscayne, Florida, is confirmed by specimens from the same lot we have in hand. We have not so far been able to have the identification of the host ascidian authoritatively established.

***Doropygus curvatus* Gray, 1938**—Described by Gray in 1938 as an associate of *Styela partita* (Stimpson) from the Woods Hole, Mass. area, this species has not been cited since its original description. Our collections in *S. partita* have shown that *D. curvatus* is the commonest ascidicolous copepod in the SW Cape Cod region and islands in terms of the proportion of ascidians infected. Of 240 *S. partita* inspected, 37 (15%) had one or more adult female copepods in their branchial baskets and 56 (23%) had either a female copepod associate and/or males and immature stages in the branchial baskets or atrial walls. Males were unknown prior to these collections. *D. curvatus* can coexist with *Botryllophilus norvegicus* in the branchial basket of a *S. partita*. *D. curvatus* is endemic to the Woods Hole region. Gray (1938) described the female of this species as follows: "Main body of the animals is the usual whitish yellow, the ovaries being darker and with a greenish tint. Eye ruby red... Eggs in the brood pouch very dark olive green, indistinguishable from black by artificial light." Our examination of the embryos and nauplii under transmitted light discloses that the embryos have a mixture of yellow-green and purple yolk and there are scattered, more superficial spots of orange and yellow. Collections of *D. curvatus* were made in *S. partita* from off Job's Neck, Naushon Island, 70′, 6/20/69; Vineyard Haven, piles near Lagoon Pond Bridge, Martha's Vineyard Island, Mass., 6′, large whaler, 7/1/69; 1 mile from Nobska Beach, Woods Hole, 41°32′48″N, 70°38′03″W, 60′–30′, SS *Verrill*, 7/3/69; off Falmouth Heights, 41°30′51″N, 70°34′55″W, 25′, SS *Verrill*, 7/3/69; off Falmouth Beach, trawl, 30′, Summers collector, 7/7/69; off Edgartown, Martha's Vineyard Island, Mass., 21′–28′, SS *Verrill*, 7/9/69; Steamship Authority Dock, Martha's Vineyard Island, Mass., 8/27/63; Nantucket Sound off Coatue Beach, north side of Nantucket Island, Mass., on a line with Nantucket standpipe and Nantucket breakwater beacon, Gray Museum specimen SEP 371, P. Schwamb collector, 8/7/64; Vineyard Sound off Falmouth Harbor, Mass., Gray Museum specimen SEP 1608, 5/26/65.

***Doropygus demissus* Aurivillius, 1885**—We obtained specimens from preserved ascidians in the Gray Museum at the Marine Biological Laboratory, Woods Hole, Mass., in old Columbia University demonstration specimens or in USFW specimens supplied by H. Plough and obtained

on the *Albatross* cruise of 8/68 in the Gulf of Maine. Males are unknown and all of the specimens were females removed from the branchial baskets of two species of *Boltenia*: records from *B. ovifera* (Linnaeus) are Gray Museum specimen SEP 1422, off Nausett Beach, Cape Cod, V. Zullo collector; Sta. 9, *Albatross* 68-12, E. of Orion Shoal, NE of Nantucket Island, Mass., 38 m, 41°26′N, 69°30′W, sandy gravel; Sta. 177, *Albatross* 68-19, S. off Penobscot Bay, Maine, 60 m, 43°44′N, 68°56′W, till; Sta. 111, *Albatross* 68-17, south of Seal Island, SW of Cape Sable, Nova Scotia, 43°14′N, 66°00′W, 40 m, shelly sand; Sta. 94, NE edge of Brown's Bank, off south end of Nova Scotia, 82 m, 42°46′N, 66°01′W; One female was removed from the branchial basket of a Columbia University specimen of *B. echinata* (Linnaeus) labelled only "Campobello" (New Brunswick, Canada). Illg (1958) examined female specimens from *B. ovifera* from the St. Lawrence Estuary, Canada, and this record was also published by Préfontaine and Brunel (1962); he recorded 8 *D. demissus* from *A. prunum* from Maine, 42°25′N; 60°08′35″W, 12 fm, 8/31/1883, *Albatross* Sta. 2064; and saw material from *B. echinata* from Plover Bay, Bering Sea, Siberia and from off Pt. Barrow, Alaska. The type locality was off Pitlekaj, Siberia, in *Cynthia* (now *Boltenia*) *echinata*. This species of copepod is a circumboreal arctic species, with the Nantucket collection being the southernmost record in the Atlantic Ocean.

***Doropygus laticornis* Wilson, 1932**—This species was discovered by Wilson in July 1924 as an associate of *Molgula manhattensis* DeKay at Woods Hole. Illg (1958) examined the Wilson holotypic female (USNM 56570) and 5 paratypic females (USNM 56571) and redescribed the species. We have collected many living animals from the Cape Cod region, all from *M. manhattensis* attached to eel grass in Sengekontacket Pond (= Long Name Pond) and piles near Lagoon Pond Bridge, Martha's Vineyard and Bass River, Cape Cod. We also removed specimens of this copepod from a Gray Museum specimen of *Molgula arenata* Stimpson SEP 862 from 35 miles east of Sapelo Island, Georgia, 30 m.

This is a southern species, with Cape Cod being the northernmost limit of its distribution. Specimens reported by Illg (1958) from *Styela partita* from the Woods Hole region have been reexamined and determined to be *D. curvatus* Gray. Records already published by Illg show that *D. laticornis* extends from Massachusetts to the Gulf of Mexico coast in Florida. Our specimens from the Woods Hole region had yellow bodies, yellow-green ova in the oviducts and yellow-green to very dark green embryos in their broodpouches. Wilson (1932) described the female specimens as having a yellow body and darker yellow eggs and illustrated one in color. Wilson (1932) described a presumed male of the species, without illustrating it. His specimens of males are unavailable. Our material has provided the first record of male dimorphism in this species. Illustrations of the two types of males are provided (Fig. 2, G and H) to demonstrate the striking differences between them.

***Doropygus schellenbergi* Illg, 1958**—We corroborate the identity from a specimen from the type lot, 11 specimens from an unidentified ascidian dredged off Georgia, 32°03′N; 79°49.5′W, 14 fm, 13 Feb. 1940, USFW Vessel *Pelican*, Sta. 181-13. No subsequent collections are known.

***Gunenotophorus curvipes* Illg, 1958**—Identification of this species, known from only a few specimens, was based on material long-preserved at the American Museum of Natural History. At the time of the original description some ambiguities in the records of the Museum and also in many manuscripts in the C.B. Wilson archives in the Smithsonian Institution caused concern. Publication of the new species had the effect of bringing forth additional information. On the basis of this, we have been able to unravel more of the record in the archives and now conclude that the type locality originally cited for the species, Bering Strait, Alaska, was wrongly attributed because of the confusion in the old records. We are sure that the type host, *Styela coriacea* (Alder and Hancock), was correctly attributed, and doubtlessly the collector was Captain R.A. Bartlett. The exact year is a bit unsure but the probable locality is somewhere off northeastern North America. We cannot confirm the occurrence of the species in the Arctic or the Pacific Oceans, although the host is a circumboreal arctic form. The Bartlett material is supported by very confused records. From what we can make out, the material was collected in 1924. Other museum specimens exist and these derive from collections made in the St. Lawrence Estuary. Some of these specimens were misidentified and some of these mistaken occurrences, cited as other species, were published by G. Préfontaine (1936). In these accounts the records for *Bonnierilla arcuata* Brément were based on specimens re-identified later by Illg as *G. curvipes*. Préfontaine specimen No. 3503, from *S. coriacea*, was catalogued as USNM 69892, with locality given as "unknown" and collection date 1930, as a type. Through the kindness of Dr. P. Brunel in 1961, at that time Biologist at Station de Biologie Marine, Grande-Rivière, Québec, access was gained to the Préfontaine records and further information is now available. USNM 69892 is from the branchial sac of *S. coriacea* (Specimen 2743 AMNH, determined by W.G. Van Name)—dredging No. 11, St. Lawrence Estuary—49°16′N; 69°08′W, 27–30 m—21 July 1932. Préfontaine specimen 3505 is from *S. coriacea* (AMNH No. 2726)—dredging No. 60—48°08′49″N; 69°37′30″W, 50 m, 21 Aug. 1933. These corrections were published by Préfontaine and Brunel (1962). We have seen another specimen, collected by Préfontaine, 1934, deposited unidentified as AMNH 1080. Material provided us in 1960 by D.P.

Abbott from *S. coriacea*, from St. Peter's Bank, off Newfoundland, USFC *Albatross* sta. 2466, 45°29′N; 55°24′W, 67 fm, 1885, first established for us definitively that we were dealing with a North Atlantic species.

***Pachypygus macer* Illg, 1958**—This species was first recorded, misidentified as *P. gibber*, by C.B. Wilson, 1927, from *Microcosmus exasperatus* Heller, collected at Spanish Water, Curaçao. Illg (1958) restudied Wilson's specimens, and with a holotype from *Styela plicata* (Lesueur), collected at Hurricane Harbor, Key Biscayne, Florida, and additional specimens from the Gulf of Mexico, 1 from an unidentified ascidian from Sarasota, Florida, and 2 from *M. exasperatus* from Sanibel Island, Florida, proposed the new species. Later collections have added a further record from Curaçao (Stock 1970).

Family ASCIDICOLIDAE Thorell, 1859
Subfamily BOTRYLLOPHILINAE
Sars *Nomen Conservandum*

***Botryllophilus norvegicus* Schellenberg, 1921 (Synonyms: *Blakeanus corniger* Wilson, 1921; *Blakeanus groenlandicus* Hansen, 1923)**—We have not been able to establish the exact publication date of the paper of Schellenberg (1921), in which he described *B. norvegicus*. Inquiries at the Trondheim Museum produced for us the information, through Mr. Tor Strømgren, that the day and month of publication are not cited in the records of the Museum, nor are they available in the files of the printer for the Museum. Wilson described the same species in a new genus as *Blakeanus corniger* on 10 June 1921. We are using Schellenberg's binomial for the species. Wilson's *Blakeanus* is undoubtedly a synonym of *Botryllophilus*, so the dating here is irrelevant. Schellenberg provided the correct generic attribution and accepting his binomial avoids for the present the formation of a new combination. However, evidence not now available to us may demonstrate the priority of Wilson's specific epithet *corniger*, producing a new combination for the species. Published records show that this species is found on both sides of the Atlantic in ascidians of the family Styelidae. It was recorded as an associate of *Pelonaia corrugata* Goodsir in Norway (Schellenberg 1921), from *Cynthia* (now *Styela*) *rustica* (Linnaeus) at West Greenland (Hansen 1923) and from "*Cynthia carnea*" (which could be either *Dendrodoa carnea* [Agassiz] or *Styela coriacea* [Alder and Hancock] in today's taxonomy) from Long Island Sound (Wilson 1921, 1932). While we have examined the Wilson type specimen and have verified its identity, we are unable to corroborate the host's identity because it was apparently not preserved. Records published by Préfontaine and Brunel (1962) list this copepod (determined as *B. groenlandicus* Hansen by C.B. Wilson) from *Polycarpa fibrosa* (Stimpson), determined by W.G. Van Name, and from *Styela mollis* (Stimpson), determined by W.G. Van Name, from the St. Lawrence Estuary. Unpublished records of Illg show this species to be an associate of *S. coriacea* from off Pt. Barrow, Alaska and from *Dendrodoa aggregata* (Rathke) at Bristol Bay, Alaska. Thus, this species is circumboreal arctic in its distribution; the Wilson (1921, 1932) record from Long Island Sound is the southernmost. All of our collections in the Woods Hole region were from *S. partita*, as follows: from Vineyard Haven, Martha's Vineyard Island, Mass., 10′, 6/12/69; from off Job's Neck, Naushon Island, Mass., 70′, 6/20/69; trawled off Falmouth Beach, Cape Cod, Mass., 30′, Summers collector, 7/9/69; Gray Museum specimen SEP 906, from Vineyard Sound off Falmouth, Mass. Harbor, 500 yds south of Bell Buoy 16, 25′-35′, V. Zullo collector, 5/26/65. Three of the 4 specimens found in the Woods Hole region shared the branchial basket of their ascidian host with females of *Doropygus curvatus*. *B. norvegicus* is a very colorful copepod. The body is yellowish, transparent, with a brick red midgut and a yellowish orange hindgut or the entire gut is brick red. White crystalline patches are symmetrically arranged under the cuticle of the cephalosome, metasome, and urosome and in the rami of the mouthparts and first through fifth legs. Ova in the oviducts are yellow, while embryos in ovisacs are transparent and have a greyish white yolk and more superficial, symmetrical orange pigment patches. Neither adults nor immature stages have an eye. Males are unknown.

***Botryllophilus* sp.**—We have removed many specimens of females of a small (average 1.3 mm) *Botryllophilus* from the branchial baskets of zooids and from the matrix of the compound ascidian *Aplidium* (= *Amaroucium*) *glabrum* (Verrill) in the Cape Cod area and in Maine, as follows: Crab Ledge off Chatham, Mass., 41°37.4′N, 69°47.5′W, 100′, SS *Verrill*, 7/16/69; 41°39.8′N, 69°48.1′W, 111′ SS *Verrill*, 7/16/69; 40°38.8′N, 69°47.8′W, 109′, 8/28/69; 40°38.8′N, 69°47.8′W, 115′, 8/28/69; Crowe Neck, Cobscook Bay State Park, Maine, −2.8′ tide, 7/31/69; Chamberlain, Maine, rocky beach off State Rt. 22, Gray Museum specimen SEP 1890, J. Reinhart collector, 8/1/69. This animal has a deep red gut, pinkish red eye and green ova in its oviducts and green embryos in its ovisacs. Detached ovisacs containing embryos are sometimes found in the ascidian's matrix. The only other records of species of *Botryllophilus* from the Massachusetts and Maine coasts, other than *B. norvegicus*, are those of Wilson (1932) and Blake (1933). Wilson (1932) reported that his specimens (from *Fish Hawk* Station 237), which he identified as *B. brevipes* Sars, 1921, were obtained from the branchial basket of a solitary ascidian *Phallusia* (now *Ascidia*) *obliqua*. Blake (1933) made note of an unidentified *Botryllophilus* which he also found in a solitary ascidian, *A. callosa*, in the Mt. Desert Island region of Maine. There are many points of resemblance between *B. brevipes* of Wilson, of which we have seen a dissected specimen (USNM 60499), and the

description of this species by Sars (1921) and with the description of *B. bergensis* by Schellenberg (1921). However, both of these Norwegian species were collected in compound ascidians (from *Botryllus* sp. and *Leptoclinides faeroensis* Bjerkan, respectively) rather than from solitary ascidians. The deficiencies of the published descriptions make it impossible for us fully to differentiate them from our considerable suite of *Botryllophilus* sp. (from the compound ascidian *A. glabrum*) and from Wilson's specimen. Such differentiation must await more adequate comparative material from Scandinavia. Should the Wilson, Sars and Schellenberg organisms, as well as the *Botryllophilus* sp. from *A. glabrum* of the northeastern United States, prove to be conspecific, it should be noted that *B. brevipes* Sars, 1921 is a junior homonym of the valid Mediterranean species *B. brevipes* Brément, 1909.

***Schizoproctus inflatus* Aurivillius, 1885**—All of the specimens we obtained were females, males, and immature stages from branchial baskets and atria of preserved specimens of *Ascidia callosa* Stimpson, supplied and identified by H. Plough: USFW 675, *Alb. IV*-66, Sta. 79, east of Pollock Rip off Cape Cod, Mass., 41°38′N, 69°28′W, 99 m, gravelly sand, 2/10/66. This is the southernmost record for this species. There is no published information on its color. Aurivillius (1885) described the female from the ascidian *Phallusia* sp. from Spitzbergen, Norway and recorded a single female of the species from this ascidian from the coast of Finmark, Norway. Sars (1921) also recorded males and females from *Phallusia* (now *Ascidia*) *obliqua* from 60 fm off the east coast of Finmark, Norway. Later published records have shown that this species ranges widely in the Arctic Ocean and it can be considered a circumboreal arctic species. It has been reported from arctic *Boltenia ovifera* (Linneaus) and *Molgula retortiformis* Verrill, as well as from *Ascidia dijmphniana* (Traustedt) and *A. obliqua*. Specimens in the USNM include a suite collected off the coast of Labrador. Those for which a host has been identified were from *B. ovifera*.

Subfamily BUPRORINAE Thorell, 1859

***Buprorus loveni* Thorell, 1859**—All of the specimens we obtained were females from the branchial baskets of preserved specimens of species of *Ascidia* supplied and identified by H. Plough: from *A. prunum* Müller: USFW 635, *Delaware* 61-19, Sta. 76, east of Cape Cod Light, 42°03′N, 60°04′W, 128 m, 11/4/61; from *A. callosa* Stimpson: USFW 675, *Alb. IV*-66, Sta. 79, east of Pollock Rip, off Cape Cod, Mass., 41°38′N, 69°28′W, 99 m, gravelly stone, 2/10/66; from *A. obliqua* Alder: USFW *Alb. IV*-64-1, Sta. 11, off Portsmouth, N.H., 98 m, silt clay, 1/17/64; USFW *Alb. IV*-63-7, Sta. 16, Fippinies Ledge, Gulf of Maine, 42°56′N, 69°26′W, 157m, glacial till, 11/15/53; ca. 25 mi east of Univ. of Georgia Marine Institute, 12 m, sandy, 31°35′N, 80°45′W, USFW, Plough collector. This is a boreal copepod on both sides of the Atlantic, known from Ascidiidae from Norway, Sweden and the Faeroes. Sars (1921) described it as "of an uniform whitish colour, with the rather large ova, contained within the incubatory cavity, of the same colour, but more opaque." "It may... easily escape attention, on account of its small size and inconspicuous colour. The mobility of the animal is almost wholly lost, the only token of life perceptible is a slight fumbling movement of the antennae and legs." Males are unknown.

Subfamily HAPLOSTOMINAE Chatton and Harant, 1924

***Haplostomides amarouci* (Blake) 1929**—Our collections of females of this copepod are from the branchial baskets of zooids or, less frequently, from the matrix of *Aplidium glabrum* Verrill from Crab Ledge off Chatham, Mass., 41°37.4′N, 69°47.5′W, SS *Verrill*, 7/16/69; 40°38.8′N, 69°47.8′W, 109′, SS *Verrill*; and from Crowe Neck, Cobscook Bay State Park, Maine −2.8′ tide, 7/31/69. These are the first reports of this species since its initial description by Blake (1929) as *Cryptopodus amarouci*, with the holotype from *Amaroucium glabrum* (now *Aplidium glabrum*) and paratypes from *Tetradidemnum* (now *Didemnum*) *albidum* (Verrill). Blake (1929) described the females as "pinkish-white, the body rather opaque. The eggs are borne in long strings and are pale-violet." Our specimens are pure white, opaque, with a light pinkish-white shiny eye. Ovisacs, containing white embryos, may be attached to females or free in the branchial baskets of zooids or in the matrix of the colony. Males are not known.

***Haplosaccus elongatus* Ooishi and Illg, 1977**—Females of this species were collected in *Aplidium glabrum* (Verrill) at Crab Ledge off Chatham, Mass., 41°39.9′N, 69°48.1′W, 111′, SS *Verrill*, 7/16/69 and from a rocky beach near Chamberlain, Maine, off Rt. 22, Gray Museum specimen SEP 1890, Reinhart collector, 8/1/69. The females are found in excavations in the matrix of the ascidian colony near its base. The female often lies on her anteriorly directed ovisacs. Detached ovisacs were also found lying in the basal matrix, either in the excavation occupied by a female or separately. The color of the animal is yellowish-white and it has a red eye and orange gut. Ova in the oviducts are light pinkish or lavender. Embryos in the ovisacs are white and have a very faint lavender-pink tint. This species was described from the coast of British Columbia in *A. glabrum* (Verrill) and in Washington State in *A. arenatum* (Van Name) by Ooishi and Illg (1977). Males are unknown.

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Publication of the "Marine Flora and Fauna of the Eastern United States" is most timely in view of the growing

universal emphasis on work in the marine environment and the crucial need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

Patricia L. Dudley first studied ascidicolous copepods as a Research Assistant to Paul Illg when she was a doctoral student in the Department of Zoology at the University of Washington in 1953. She chose to work on the life cycles of copepods of the family Notodelphyidae for her Ph.D. thesis (1957). For two post-doctoral years she travelled to European marine labs and the Hawaii Marine Laboratory, collecting symbiotic copepods of the Ascidicolidae and Notodelphyidae and studying their development. In 1959, she became associated with the Department of Biological Sciences, Barnard College, Columbia University, where she still teaches as a Professor of Biology. During her tenure at this college and numerous summers at the Friday Harbor Laboratories of the University of Washington, she has continued to study ascidicolous copepods, adding electron microscopy of internal structures of copepods, other crustaceans and Mesozoa as subjects of interest. During the summers of 1969 and 1970 she was associated with the Systematics-Ecology Program, Marine Biological Laboratory at Woods Hole and collected many of the ascidicolous copepods upon which this manual is based.

Paul L. Illg first encountered ascidicolous copepods among the rich fauna at the Friday Harbor Laboratories during the summer of 1939, while he was a graduate student at the University of California, Berkeley, California. Some of the material was presented in a thesis offered for the M.A. degree, 1941. During tenure as an associate curator, U.S. National Museum, he resumed studies on the material and was able to augment the collections by a stay at Friday Harbor during the summer of 1950. Material from the east coast was also incorporated in his monographic studies. The completed study, offered as a thesis to qualify for the Ph.D. degree in 1952 at the George Washington University, was subsequently published by the U.S. National Museum (1958).

During his tenure at the Museum he acquired a fairly wide acquaintance with copepods, free-living and symbiotic. In 1952, acceptance of an offer from the University of Washington returned him to the Northwest where, with a succession of students, he continued studies on taxonomy, life history and biology of copepods, retiring as Professor Emeritus in 1982. An invitation from the Boston University Marine Program and the Systematics-Ecology Program of the Marine Biological Laboratory in 1969 brought him to Woods Hole where a substantial amount of his research time was devoted to the copepods which are the subject of this manual.

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